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NUTRITION OF SPRUCE GROUSE OF THE SWAN HILLS, ALBERTA

BY



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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Nutrition of Spruce Grouse of the Swan Hills, Alberta" submitted by Bruce Alexander Pendergast in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Nutrition of spruce grouse (*Canachites canadensis*) in the Swan Hills region of Alberta was investigated through studying the habitat, gut tract contents and organ weights of 195 birds collected in all months of the year, and through feeding experiments with birds kept in captivity.

During that part of the year when the ground was covered by snow, the food of spruce grouse consisted of 99 per cent lodgepole pine (*Pinus contorta*) needles and 1 per cent spruce (*Picea* spp.) needles. Berries of bog cranberry (*Vaccinium vitis-idaea*) ripened in the previous year, were consumed as soon as they were snow free. Buds of white spruce (*Picea glauca*) were the first new growth utilized in spring and like other new growth were found to be rich in protein. Very little new vegetation was available until July, well after laying was completed. In summer and fall the main foods were leaves, flowers and berries of tall bilberry (*Vaccinium membranaceum*), and berries of bog cranberry. The high utilization of bog cranberries by breeding females and chicks, raises a question of the importance of these berries to the distribution and numbers of spruce grouse.

The winter diet is low in some minerals that may be supplemented by minerals in grit which was consumed in large quantities. Grouse with access to soil were kept up to two months in captivity without weight loss on a diet of pine needles. The gross energy of pine needles



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was quite high at 5.24 Kcal per gram. On the other hand, the metabolizable energy was less than one third of this value because of the high content of indigestible crude fiber in the food. The crude fiber of the winter food was not digested to a significant degree and was handled by an increase in the capacity of the gut tract in winter, and by a separation of constituents of the food by the ventriculus. The protein content of winter food was only 8.25 per cent but the metabolizable energy-protein ratio and the daily energy intake were adequate for body maintenance. Most amino acids of pine needles were in sufficient quantity to meet requirements for maintenance.

Food in all seasons appeared superabundant. The grouse studied selected favored food items from several potential foods available. Growth and moulting occurred when foods in addition to pine needles were available. During reproduction the only foods available were conifer needles and over-wintered bog cranberries.

Growth of wild birds stopped at roughly the same time as in captive birds consuming formulated rations, suggesting that the diet of the wild birds was near an optimum for growth.

Birds collected in winter appeared to be in better physical condition than those collected in July and August, further indicating that the winter food was not likely to be controlling the numbers of individuals in the population.

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examined samples from wild birds for parasites. Miss T. M. Delane allowed me to use pens which she had spent time constructing. I also acknowledge the benefit of observations and ideas gained from the other students of spruce grouse at the University of Alberta, K. H. McCourt, R. L. McLachlin and R. P. Stoneberg. My mother's assistance in proofreading was appreciated. Above all I thank my wife who not only helped in the field and in preparation of the manuscript but also provided the encouragement required in such a project.

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INTRODUCTION

The role that food plays in population regulation has received considerable attention. Lack (1966) in summarizing studies of avian populations concluded that food was the ultimate controlling factor.

Food as a controlling factor can affect birds at several stages of the life history of the individual. Though much of Lack's evidence is derived from studies of nidicolous forms where the young are dependent on food brought them by their parents, he also refers to studies of nidifugous red grouse (*Lagopus scoticus*) and willow ptarmigan (*Lagopus lagopus*) done by Jenkins and Watson in Scotland. Jenkins (1963) found that the main controlling factor to population size was the breeding density, as determined by territory size, which he showed to be dependent on food supply in fall. He felt that breeding success, though also affected by food, was not critical to the population since a surplus of young was produced even in bad years. This refutes Siivonen's (1957) hypothesis that the controlling factor in tetraonid populations was the success of reproduction. He showed a correlation of early spring temperatures and population fluctuations in European tetraonids and concluded that early spring growth was critical to health of females and through them the chicks. Zwickel (1965), on the other hand, found no evidence for this hypothesis while studying a population of blue grouse (*Dendragapus obscurus*) on Vancouver Island.

Bump *et al.* (1947) in reference to ruffed grouse (*Bonasa umbellus*), and Boag (1964) in reference to blue grouse point out that the quantity of food was unlikely to be controlling tetraonid populations since it appears superabundant. Koskimies (1955), Lauckhart (1957), and Boag (1964) suggested that quality rather than quantity of winter food may be critical to adult survival and/or egg quality and thus chick survival.

Lauckhart (1957) suggested that the quality of conifer browse could change when these trees periodically set seed, thus affecting the health of the animals feeding on them. Lodgepole pine (*Pinus contorta*) on which the spruce grouse (*Canachites canadensis*) in the region studied feed heavily in the winter, sets seed fairly regularly (Crossley, 1955). Furthermore, there is no evidence that the food of ruffed grouse fluctuates in quality and it has been found adequate for winter maintenance (Treichler, 1946).

It is apparent that the nature and importance of diet of tetraonids in the control of their numbers remains unanswered.

In launching this study, the hypotheses were made: 1) that winter food would be found to be marginal in some of the critical nutrients, and 2) that some members of the wild population would show signs of starvation or malnutrition. In investigating these hypotheses, the year round diet, the nutritional quality of the major food items, and the ability of spruce grouse to utilize the food items consumed were considered.

This study was undertaken in an effort to elucidate the role of nutrition in the regulation of population density in one species of tetraonid. The spruce grouse was chosen as the subject of investigation because, for much of the winter, it was reported to be monophagous (Ellison 1966). This simplified a qualitative study of the birds' diet and made digestibility studies using the natural food easier.

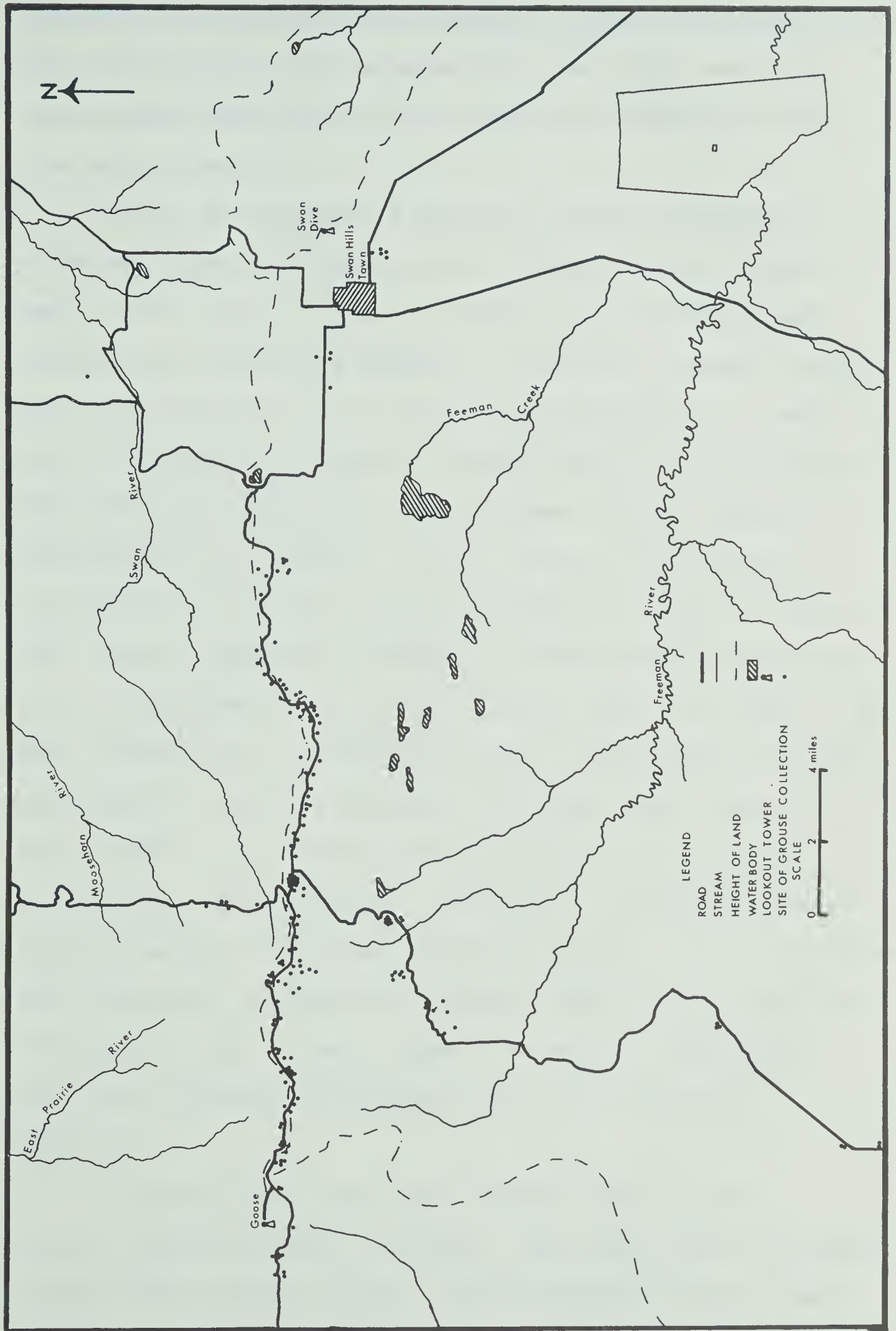
DESCRIPTION OF THE STUDY AREA

Field work was conducted in the Swan Hills region of Alberta, approximately 150 miles northwest of the city of Edmonton. Investigations were concentrated along an access road constructed by the provincial Department of Lands and Forests, Province of Alberta, running from five miles northwest of Swan Hills' town site to a fire look-out tower on Goose Mountain, approximately thirty miles west (Fig. 1). The road roughly follows a ridge with an elevation of about 4,500 feet, which is the main axis of the plateau from which the Swan Hills were derived. Drainage to the north is into Lesser Slave Lake and to the south is into the Athabaska River.

"The Swan Hills are remnants of a maturely dissected upland which represents residuals of erosion from the preglacial plains level.....
.....Overlying the Paskapoo formation on the summits of the upland, there is a bed of coarse gravel which consists almost entirely of water-worm pebbles of pure white quartzite up to 6 inches in diameter." (Allan 1919, pp. 8 and 12).

Allan further explains how vegetation types in the

Figure 1. Area from which spruce grouse were collected.



area are reflections of the subsoil. Where sandstone is near the surface, pine predominates, but bogs and sedge meadows are found even on the summits of mountains where drainage is poor.

Except in the bogs, alpine fir (*Abies lasiocarpa*), lodgepole pine, and white spruce (*Picea glauca*) comprise most of the trees. The tree species are usually mixed, though pure stands are present. Alpine fir appears to be the climax tree as it is the only species which is reproducing abundantly. The most common shrub is tall bilberry (*Vaccinium membranaceum*). Less common is bog cranberry (*Vaccinium vitis-idaea*). In dry natural openings and artificial clearings, red elder (*Sambucus pubens*), mountain ash (*Sorbus scopulina*), blueberry (*Vaccinium myrtilloides*), birch (*Betula* sp.), and sedges (*Carex* spp.) are found. The most common herbs of forested areas are bunchberry (*Cornus canadensis*) and *Rubus pedatus* (no common name listed by Moss, 1967). Less common herbs include twisted stalk (*Streptopus amplexifolius*), twinflower (*Linnaea borealis*), green-flowered wintergreen (*Pyrola virens*), and false mitrewort (*Tiarella trifoliata*). Mosses (*Musci* spp.) comprise the ground layer in most areas. Horsetails (*Equisetum* spp.) and clubmoss (*Selaginella* spp.) are locally abundant.

In wetter areas, the most common tree is black spruce (*Picea mariana*). Labrador tea (*Ledum groenlandicum*) is the most abundant shrub. Typical herbs include cloud-

berry (*Rubus chamaemorus*) and small bog cranberry (*Vaccinium oxycoccus*).

Vegetation in areas described by Allan (1919) as tundra consist mainly of mosses and sedges with smaller numbers of small bog cranberries and mountain laurel (*Kalmia polifolia*).

METHODS

As a first step in understanding the nutrition of spruce grouse, the year round diet of the species had to be determined in the area concerned. The diet was investigated by collecting birds in the wild on a monthly basis and recording the contents of their crops.

An average of 9 spruce grouse, more than 6 months of age, were shot each month, from June 1967 to October 1968. An average of 15 grouse, less than 6 months of age (birds of the year), were collected each month from July to November of 1967 and 1968. Age of the latter group was determined by the presence of a bursa of Fabricius. From December 1 on, all birds were considered adults for the purposes of this study. Appendix I shows the number of birds collected each month. Field work was conducted during trips of two to ten days into the study area. Time spent in the field is also shown in Appendix I.

The types and quantities of foods utilized were determined by examination of the crop contents. Plant material was identified with the aid of Moss (1967).

Volumes before and weight before and after freeze-drying were determined for each type of food. Data were tabulated by the aggregate volume and weight method of Martin *et al.* (1946). Frequency of occurrence was also included.

Foods utilized were compared to foods available. This was determined by analyses of vegetation at 60 sites where grouse were collected. A 50-square meter plot was used. The species of trees included in the plot were recorded and placed in the following size classification: under 0.5 dm diameter at breast height (d.b.h.) and between 1 dm and 1 m tall, under 0.5 dm d.b.h. but over 1 m tall, 0.5-1.0 dm d.b.h., 1-2 dm d.b.h., 2-3 dm d.b.h. and 3-4 dm d.b.h. The ground vegetation was analysed on ten 0.1 square meter plots, according to a method outlined by Daubenmire (1959). The 0.1 square meter plots analysed were selected from the 50-square meter plot by a method devised by McLachlin (pers. comm.).

Food types from crops were combined to give samples of 10 grams dry weight for analyses of chemical constituents and gross energy. Additional samples were obtained by collecting specific food items in the field.

Food samples were analysed for the following: residual moisture, crude fiber, sodium, phosphorus, calcium, magnesium, potassium, and lignin by the Alberta Soil and Feed Testing Laboratory. The gross caloric value was measured with a Parr oxygen bomb calorimeter. Amino acids present in pine needles were analysed by the Department

of Biochemistry, University of Alberta. Eight samples were prepared for these analyses by a method described by Moore and Stein (1963).

The utilization of the nutrients present in the winter diet of spruce grouse was investigated. Contents were removed from various parts of the gut tract and were analysed as described for the foods.

Additional information on digestibility of pine needles was obtained using captive birds. Birds were captured alive by noosing (Zwickel and Bendell, 1967) and kept in captivity for up to fifteen months. Live birds were held in outdoor pens with access to shelters. Pine needles, twenty per cent protein turkey grower, grit and water were provided *ad libitum*.

In determining the efficiency of digestion of pine needles, birds were placed in 20" x 40" x 20" cages to enable measurement of intake of needles and output of feces. Samples of food, caecal, and intestinal feces were analysed as described above for foods.

In assessing the adequacy of the diet, a comparison was made of the general condition of birds collected throughout the year. Condition was determined from total weight of birds, and weight of *pectoralis* muscles, liver and heart.

Morphological adaptations to the changing diet were determined from the following measurements of internal organs of birds sampled throughout the year: weights, with

and without contents of the crop, proventriculus, ventriculus and large intestine; weights, with contents, of a caecum and small intestine; weights of liver, heart and pancreas; and lengths of small intestine, a caecum, and large intestine with cloaca.

Searches of adjacent areas and comments of local people indicated that the study area had a high population which was near a peak in 1967-68.

Significance was measured by the t-test (Steel and Torrie, 1960). Five per cent and one per cent levels were considered significant and highly significant respectively.

RESULTS AND DISCUSSION

1. The diet

Adults

The food items recorded in crops of spruce grouse collected from June 1967 to September 1968 are presented in Table I. The volumes and dry weights are included to facilitate comparison with other investigations.

Average volumes and weights of the contents of crops were greater in the winter months of November, December, January, and February than in the summer months of May, June, July and August (Table I). More than one factor may be involved in this change. Irving *et al.* (1967) found in willow ptarmigan that maximum crop weights were recorded when day length was least, the crop acting as a food reservoir during the long winter night. Thus the chances of collecting birds with full crops are greater in winter.

Table 1. Contents of 99 crops of spruce grouse over 6 months of age collected on a monthly basis in the Swan Hills, Alberta.
(t indicates a trace--less than 0.01 g or 0.1%).

Months of year		1			2			3			4			5			6			7			8			9			10			11			12		
Number of crops		2			15			9			4			11			10			14			9			9			3			8			5		
Volume of contents (cc)		11.8			5.2			5.5			4.9			4.0			4.5			4.1			4.9			5.2			4.5			3.5			13.4		
mean		11.5-12.0			0.1-15.0			0.1-16.4			0.1-12.9			0.1-8.2			0.1-22.5			0.14-20.0			4.2-7.6			2.5-9.6			0.1-12.9			0.5-8.0			2.9-27.5		
range		4.2			2.0			2.1			2.0			1.5			1.1			1.0			1.1			1.0			0.7			1.7			5.5		
Dry wt. of contents (g)		3.8- 4.6			0.0- 6.2			0.0- 7.4			0.0- 3.9			0.0- 4.4			0.0- 4.0			0.0 - 8.7			0.1-2.4			0.5-2.8			0.0- 2.1			0.2-4.2			1.5- 8.9		
		% Dry wt.			% Freq.			% Dry wt.			% Freq.			% Dry wt.			% Freq.			% Dry wt.			% Freq.			% Dry wt.			% Freq.			% Dry wt.			% Freq.		
temized crop contents		Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.			Vol.		
Part utilized		wt.			wt.			wt.			wt.			wt.			wt.			wt.			wt.			wt.			wt.			wt.			wt.		
Unidentified fungi	sporocarp																																				
Musci	spore cases																																				
<i>Equisetum</i> spp.	stems and tips																																				
<i>Pinus contorta</i>	needles	100	100	100	99.3	97.5	100	66.5	72.0	89.0	44.1	59.5	75.0	44.2	39.0	72.7	13.4	24.3	10.0																		
<i>Picea</i> spp.	needles				0.3	0.4	13.3	24.3	22.8	22.2	t	t	25.0	22.8	27.4	36.4	65.3	58.9	40.0																		
Gramineae	leaves																t	t	10.0	0.1	0.1	7.1															
<i>Carex</i> spp.	seeds																																				
<i>Streptopus amplexifolius</i>	flowers																																				
	berries																																				
<i>Betula</i> spp.	flowers																0.7	0.4	10.0																		
<i>Tiarella trifoliata</i>	flowers																																				
<i>Rubus chamaemorus</i>	berries																																				
<i>Cornus canadensis</i>	leaves																																				
<i>Vaccinium membranaceum</i>	leaves																12.0	10.9	50.0	34.6	45.1	100.0	10.1	11.6	55.5	4.1	3.5	33.3				t	t	12.5			
	flowers																1.6	0.7	20.0	4.9	2.5	50.0															
	berries																																				
<i>Vaccinium myrtilloides</i>	berries																																				
<i>Vaccinium vitis-idaea</i>	leaves																																				
	new berries																																				
	old berries																																				
<i>Taraxacum officinale</i>	leaves																																				
Arthropoda	entire																																				
Grit	entire				0.4	2.1	46.6	0.6	1.4	33.3	0.5	3.3	25.0	2.7	21.7	54.5	0.1	0.5	10.0	0.4	2.6	14.2	2.3	12.3	44.4	0.7	9.2	66.7				1.8	6.5	12.5			

Another possibility is that basal metabolism may be increased as part of acclimatization in winter as shown by Delane (1968) in pheasants (*Phasianus colchicus*). Such an increase might require a greater intake of food. Furthermore, the food consumed during the winter months contains a high proportion of indigestible material (shown by experiments described later) thus requiring an increased consumption even if energy needs do not change.

Conifer needles comprised 62 per cent of the dry weight of the yearly diet of the spruce grouse sampled. For several months in the winter, conifer needles are the only source of energy in the diet. Hence the winter diet is virtually monophagous while the summer diet by contrast is more varied and derived in the main from ground vegetation and a few arthropods.

Grit was consumed in all seasons and in larger quantities than has been reported for other tetraonid species, for example blue grouse (Boag, 1963) and capercaillie (*Tetrao urogallus*) (Zwickel, 1966).

One reason for large quantities of grit in crops is that many grouse were collected while they were consuming it on roads. It is also probable that birds may derive minerals from grit, as has been shown in pheasants (Sadler, 1961). Soil, which may have been consumed for its minerals, was found in the gut tracts as well as the crops of some birds.

If one examines the year round diet on a month to

month basis, it becomes apparent that, excluding grit, the food during the months of November through February was 99 per cent pine needles and 1 per cent spruce needles by dry weight. Ellison (1966) also found that conifer needles supply all of the winter food of spruce grouse in Alaska.

In March 1968, bog cranberries, ordinarily covered by snow, were accessible because of an unusual thaw. The fact that cranberries were consumed in March shows that spruce grouse will take advantage of an unusual situation to add variety to their diet. Spruce needle consumption increased in March but not by a significant amount.

In the spring months of April and May, conifer needles still comprised the bulk of the diet agreeing with Ellison's (1966) study in Alaska and Stoneberg's (1967) observations in Montana. Spruce needles increased significantly in percentage weight of crop contents during these months and cranberries were recorded in increasing amounts as snow melted.

Several factors could account for the increase in spruce needle utilization in April and May. Ninety-nine per cent of the spruce needles taken in April and May were consumed by females which put on weight prior to laying, suggesting that spruce may provide some nutrients needed at that time. King (1968) also found a difference between male and female blue grouse diets in spring. Hill and Dansky (1954) showed that domestic chickens, if given only

one source of food, consume to meet their energy requirement, even if this means being deficient in protein. On the other hand, if a choice of foods is offered domestic chickens, protein is consumed at a level near the experimentally derived optimum (Funk, 1932). The evidence is conflicting as to whether blue grouse can select for protein level in conifer needles. Hoffman (1961) reported that blue grouse consumed needles from the region of trees where the protein level was greatest. Boag and Kiceniuk (1968), however, found no evidence that the needles of trees fed on by blue grouse were higher in protein than those in other areas. Korschgen (1966) found that the protein intake of ruffed grouse also corresponded to their needs, which he assumed were greater during growth, moult and for females during breeding. It is possible that the requirements for protein and calcium in spruce grouse prior to laying, may be met by a combination of spruce and pine needles, better than by pine alone, and that the females are able to select the best combination.

A behavioral explanation involving dispersion could also account for the increase in spruce needle consumption. During fall and winter, until March, spruce grouse were observed in groups as large as ten birds (Table 2). From March on, only singles and pairs were seen. Spring territorial behavior, as shown by Jenkins (1963) in red grouse could have forced some birds into habitats where pine was less available and hence birds were forced to utilize spruce needles.

Table 2. Sizes of groups of spruce grouse seen during
1967 and 1968 in the Swan Hills, Alberta.

Month	Size of Group				
	1	2	3-4	5-7	7+
January	2	1			
February	4	2	2	1	1
March	10	1			
April	1	1	1		
May	15				
June	9	2			
July	7	2	6	3	1
August	5		2	7	1
September	3		5		6
October	5	2	1	4	5
November	5	1	3	1	5
December			1		

June was a month of transition in diet from conifer needles to ground vegetation. Over-wintered bog cranberries remained important in the diet. Spruce needles were utilized more heavily than pine in June. Much of this spruce was new growth, a preference reported by Ellison (1966). The crop of an incubating female, collected from the nest on June 24, 1968 contained 22.5 ml of "new leaders" of spruce. McCourt (pers. comm.) observed two female spruce grouse during their incubation period feeding selectively on spruce leaders.

New growth of horsetails and bilberries were also utilized in June. New growth may be selected because of its tenderness and possibly because of a high protein content as was shown in new spruce needles by nitrogen analysis.

In July ground plants provided the food sources with bilberry leaves and over-wintered bog cranberries the two most utilized forms.

During August and September the new berries of all species of *Vaccinium* and seeds of sedges (*Carex* spp.) became important. Spruce needles were found in the crop of one bird in August, indicating that some individuals may utilize conifer needles all year round. It has been suggested that grouse when a hunter is present will undertake displacement feeding and therefore the presence of needles in the crop of a bird shot in the summer may be an artifact (Ellison, 1966). Such was not the case in the

present study, as the bird containing the spruce needles was collected while dust bathing.

The collection of only three crops of adults in October probably gave an incomplete picture of the diet, but a partial return to conifer needles was indicated. Crichton (1963) and Ellison (1966) found that conifer needle consumption increased in fall, but needles were not relied upon exclusively until after snow covered the ground vegetation. Sporadic snowfall occurred on the study area from September onward with a permanent cover falling during the night of October 21, 1967. Birds were not collected subsequently until November when, as already stated, conifer needles were the only items recorded.

Birds of the year

Table 3 presents the food items recorded in the analysis from the crops of birds less than 6 months of age.

The increase in contents per crop with age reflects the growth of juveniles as well as the possible reasons already mentioned for the increase in crop contents of adults during fall.

The main foods utilized by the juveniles were the same as for adults, once they were two weeks of age and had become basically herbivorous. As shown by Boag (1963) in blue grouse, the variety of foods eaten by juveniles was greater than by adults. Also the major foods were utilized in different proportions.

On a dry weight basis, the most important food for

Table 3. Contents of 65 crops of juvenile spruce grouse collected in the Swan Hills, Alberta. (t indicates a trace--less than 0.01 g or 0.1%).

Months of year		7	8			9			10			11				
Number of crops		8	8			22			16			11				
Volume of contents (cc)		mean range	0.4 0.2-1.1	2.2 0.1-3.2			7.2 1.4-17.5			3.1 0.1-7.5			7.4 t-15.1			
Dry wt. of contents (gm)		mean range	0.1 t-0.2	0.7 0.2-2.3			1.9 0.4-6.0			1.0 0.1-4.9			3.7 t-9.8			
Itemized crop contents	Part utilized	% Vol.	% Dry wt.	% Freq.	% Vol.	% Dry wt.	% Freq.	% Vol.	% Dry wt.	% Freq.	% Vol.	% Dry wt.	% Freq.	% Vol.	% Dry wt.	% Freq.
Unidentified fungi	sporocarp							0.8	0.5	18.1	0.4	0.2	6.3			
Musci	spore cases				0.6	0.3	25.0	t	t	9.1						
<i>Equisetum</i> spp.	stems and tips	3.7	3.7	25.0	2.3	0.9	37.5	9.0	5.0	59.0	3.4	3.7	18.8			
<i>Pinus contorta</i>	needles										4.6	5.3	37.5	92.5	97.3	100.0
<i>Picea</i> spp.	needles										20.1	26.6	18.8			
<i>Abies lasiocarpa</i>	needles							t	t	4.5						
<i>Larix laricina</i>	needles										t	t	6.3	t	t	9.1
<i>Carex</i> spp.	seeds	0.3	0.6	12.5	30.5	26.3	75.0	11.5	15.9	84.3	7.7	6.2	18.8	0.4	0.2	9.1
Gramineae	leaves							t	t	4.5				0.1	t	9.1
<i>Streptopus amplexifolius</i>	flowers berries				4.3	2.2	25.0	1.0	0.5	27.2						
<i>Betula</i> spp.	flowers															
<i>Tiarella trifoliata</i>	seeds							0.4			1.2	1.0	6.3			
<i>Rubus chamaemorus</i>	berries				10.4	5.6	12.5	3.4	2.8	22.7	0.3	0.1	6.3			
<i>Rubus strigosus</i>	berries							t	t	4.5						
Leguminosae	leaves										0.1	0.1	6.3			
<i>Cornus canadensis</i>	leaves										t	t	6.3			
<i>Pyrola virens</i>	seeds							0.4	0.4	4.5						
<i>Vaccinium membranaceum</i>	leaves flowers berries	7.7	15.0	25.0	2.4	1.2	12.5	1.0	1.6	22.7	3.5	2.4	37.5			
<i>Vaccinium myrtilloides</i>	berries leaves				15.6	9.0	25.0	25.7	14.4	18.1	12.8	6.0	31.3			
<i>Vaccinium vitis-idaea</i>	leaves new berries old berries							33.4 0.1	19.7 t	36.3 4.5	9.3	3.5	18.8			
					7.2	4.3	37.5	3.9	2.9	22.7	31.8	17.3	62.5	7.0	2.5	9.1
		66.0	45.1	62.5	13.3	2.4	25.0									
Arthropoda	entire	22.0	31.4	88.5	7.0	3.9	50.0	t	t	27.7						
Pulmonata	entire							0.6	1.0	9.0	t	t	6.3			
Grit	entire	0.3	4.1	12.5	6.4	43.8	25.0	4.9	35.3	59.0	4.9	27.5	56.2			

juveniles in July was over-wintered bog cranberries, though arthropods had a higher frequency of occurrence. Arthropods were consumed exclusively in the first week of life only, as noted by Klebenow and Gray (1968) in sage grouse (*Centrocercus urophasianus*) and Bump *et al.* (1949) in ruffed grouse. During August the dietary items were similar to those of adults though insects were still utilized more by juveniles, as were sedge seeds. In September, insect consumption fell to the adult level, but sedge seeds remained relatively more important for young birds. As with the adults, all new *Vaccinium* spp. berries became very important in these months. In October juveniles began taking pine and spruce needles and the consumption of grit increased greatly. Larch needles found in crops were from birds taken off of the main study area.

The snails (Suborders, Orthuretha and Sigmurethra) consumed by juveniles are taken in quantities too small to be of importance in their nutrition. However, they may be intermediate hosts for such trematode parasites as *Urogoninum* sp. and hence a source of infection for grouse (Holmes and Boag, 1965).

The utilization of insects by very young birds is probably associated with a high dietary protein requirement as shown in Japanese quail (*Coturnix* sp.) (Weber and Reid, 1967), in bobwhite quail (*Colinus virginianus*) (Baldini *et al.*, 1950) and in ruffed grouse (Bump *et al.*, 1949). The differences between the diet of juveniles and

adults in September and October, as reflected by the greater use of sedge seeds, was probably related to the continuing high protein requirement of juveniles. Sedge seeds were shown by nitrogen analysis to be one of the best sources of protein of foods utilized.

There may be several reasons for the greater diversity in the diet of young birds. Firstly, the sample of juveniles was larger than that of adults and may have included more types of material taken by only a few birds, for example, snails, cloudberry, larch needles, etc. Secondly, the requirements of growing birds may differ from that of adults and the young may be able to select foods to meet the nutrient demands of growth. Juvenile spruce grouse may consume extra grit in fall to obtain minerals. The lack of grit in the crops of birds collected in November probably reflects the fact that the sources of grit were covered by snow and remained so covered until winter thaws and snow ploughing of roads exposed patches of ground.

2. Food preference

Tables 4 and 5 show coverage and frequency data for ground vegetation and the three tree species in areas where 60 adult grouse were collected. Comparison of these tables with Tables 1 and 3 gives a general picture of the degree of selection of food types by spruce grouse.

Table 4 shows that mosses are almost ubiquitous. The part utilized by grouse (spore capsules), however, occurred

Table 4. Distribution of ground plants present at points in the Swan Hills where 60 adult spruce grouse were collected. Average per cent cover is based on 600 0.1 square meter plots in 60 areas.

Plant types	Per cent cover of ground plants	Per cent occur- rence in 0.1 square meter plots
<i>Musci</i> sp.	72.79	91.4
<i>Vaccinium membranaceum</i>	9.71	51.0
<i>Rubus pedatus</i>	9.10	63.1
<i>Cornus canadensis</i>	7.21	58.6
<i>Vaccinium vitis-idaea</i>	4.90	40.7
<i>Ledum groenlandicum</i>	4.85	24.0
<i>Vaccinium myrtilloides</i>	4.33	17.8
<i>Lycopodium</i> spp.	1.91	18.4
<i>Gramineae</i> spp.	1.83	9.3
<i>Carex</i> spp.	1.58	4.1
<i>Pyrola</i> spp.	1.39	16.0
<i>Linnaeae borealis</i>	1.36	23.1
<i>Rubus chamaemorus</i>	1.31	4.3
<i>Equisetum</i> spp.	.98	6.2
Lichen	.93	7.1
<i>Streptopus amplexifolius</i>	.75	6.5
<i>Epilobium angustifolium</i>	.47	1.9
<i>Geranium</i> sp.	.29	5.5
<i>Arnica cordifolia</i>	.17	.3
<i>Tiarella trifoliata</i>	.14	.3

Table 5. Distribution of tree species present on 50-square meter plots where 60 adult spruce grouse were collected in the Swan Hills, Alberta.

Size class	<i>Pinus contorta</i>		<i>Picea</i> spp.		<i>Abies lasiocarpa</i>	
	Per cent of plots trees found in	No. of trees per 50 square m plot	Per cent of plots trees found in	No. of trees per 50 square m plot	Per cent of plots trees found in	No. of trees per 50 square m plot
0-1 m tall	3.3	0.0	18.3	1.1	63.3	14.7
>1 m tall						
<0.5 dm d.b.h.	1.7	.0.0	18.3	0.8	35.0	0.9
>0.5-1 dm d.b.h.	16.7	0.4	33.3	0.8	28.4	0.8
>1-2 dm d.b.h.	53.3	1.9	33.3	1.4	38.3	1.1
>2-3 dm d.b.h.	53.3	.1.1	18.3	0.5	33.3	0.5
>3-4 dm d.b.h.	8.0	.0.1	-	-	1.7	0.1
>4-5 dm d.b.h.	-	-	1.7	0.0	-	-

only in patches and for a short period of time. Bilberry was common and provided berries which were heavily utilized and the only leaves utilized in large quantities. Bog cranberry leaves were not utilized though the berries were consumed over a longer period of time than any other ground food, and were often utilized in large quantities. As many of the cranberry plants bore little or no fruit, the coverage figures indicate a greater abundance than was true for berries. Sedges, most common on roadsides, produced seeds that were selected by grouse (1.58% cover vs. 26% of the dry weight of juvenile crop contents). On the other hand, some abundant plants such as *Rubus pedatus* and bunchberry were almost completely ignored by the grouse though both provided abundant fruit in 1967.

Table 5 shows the tree species in the plots where ground vegetation was analysed. Alpine fir is by far the most common tree under 0.5 dm diameter at breast height. Among trees over 0.5 dm diameter at breast height pine, spruce and fir were all common. Spruce was apparently preferred for roosting as droppings were most abundant under it. In spite of its abundance alpine fir was not utilized for food. Considering its abundance spruce was utilized only sparingly for food from November to February although it was utilized to a greater degree in May and June.

Selection of foods by animals can be interpreted in

two ways. If the types and abundance of food which the animal is selecting among are similar such as conifer needles or berries and if the one not utilized is acceptable in other areas, the selection is probably a result of simple preference and not dietary need. Such selection also indicates that food in general is probably abundant, otherwise all edible foods would be taken. Selection of bilberry leaves and berries over bunchberry and *Rubus pedatus* would appear to be in this category. Bunchberries were never found in grouse crops though they were reported in small quantities from spruce grouse in Alaska (Ellison, 1966) and are a favorite food of ruffed grouse in New York (Bump *et al.*, 1959). When considering the winter diet of spruce grouse, selection of pine needles over spruce and fir would appear to be a preference also and not of nutritional necessity as spruce grouse were recorded consuming nothing but spruce needles in the winter in a part of Alaska where pine was unavailable (Ellison, 1966). Furthermore, Stenlund and Magnus (1951) reported that spruce grouse in Minnesota eat balsam fir (*Abies balsamea*) needles, a species very similar to the alpine fir, which was not utilized in the Swan Hills. Ruffed grouse have also been reported to select different foods in different areas (Bump *et al.*, 1959).

Food selection may have a different significance where the food type is selected by the species in different areas and no comparable alternative is available. In this

case, food selection may be for a nutrient not found in the rest of the diet. Selection of over-wintered bog cranberries may be of this type. In July juveniles appeared highly dependent on this food (Table 3) as it was the only berry present. Similarly if females in breeding condition require a different diet than for maintenance, they may be dependent on cranberries as a supplement to conifer needles. Since so few food types are available to breeding females, or are utilized by the young in July, and since both rely heavily on over-wintered berries, such berries may be important in the numbers and distribution of spruce grouse.

3. Analyses of foods

Table 6 shows the results of analyses of the main foods of spruce grouse throughout the year. In general, summer foods are lower in crude fiber and higher in protein than winter foods. Korschgen (1966) observed that similar seasonal changes occurred in the diet of ruffed grouse and corresponded with changes in protein needs of the species throughout the year.

There was no indication that foods chosen by grouse were higher in nutrients than those picked by hand. The lowest protein content (4.41%) for pine needles was found in a crop sample. The needles in this sample, taken in December, were yellowish and appeared to be from an unhealthy tree. Boag and Kiceniuk (1968) showed a similar lack of selection for protein in pine needles by spruce

Table 6. Chemical analyses and gross energy values of foods utilized by spruce grouse in the Swan Hills, Alberta. Values for samples greater than one are averages.

	Sample size	Gross energy Kcal/g	Per cent of dry weight						
			lignin	Crude fiber	Protein (Nx6.25)	Ca	P	Mg	K Na
<i>Musci</i> spp. capsules	1	4.33	12.2	27.8	8.8	.08	.08	.03	.40 .06
<i>Equisetum</i> spp. stems and tips	1	4.26	-	-	17.6	-	-	-	-
<i>Pinus contorta</i> needles	16	5.32	26.2	41.7	8.2	.14	.12	.11	.52 .22
<i>Picea</i> spp. needles	2	5.19	16.3	30.9	5.8	.43	.10	.07	.39 .12
needle buds	2	4.89	22.0	29.5	16.8	.08	.15	.04	.55 .07
<i>Carex</i> spp. seeds	1	5.15	-	-	15.0	-	-	-	-
<i>Streptopus amplexifolius</i> green berries	1	-	-	-	19.0	-	-	-	-
<i>Vaccinium membranaceum</i> leaves	2	4.97	12.6	22.9	14.3	.18	.10	.11	.64 .06
flowers	1	5.10	-	-	18.3	-	-	-	-
green berries	1	5.07	-	-	11.7	-	-	-	-
ripe berries	1	4.95	22.9	37.7	10.1	.15	.24	.10	1.03 .41
<i>Vaccinium vitis-idaea</i> new berries	1	4.70	12.2	20.4	3.8	.04	.05	.02	.27 .05
over-wintered berries	1	4.91	22.1	34.5	5.1	.10	.14	.08	.11 .21

grouse and blue grouse in southwestern Alberta.

The average level of protein in the needles of pine in the area studied was 8.25 per cent (dry weight) which compares closely to the 7.5 per cent protein (dry weight) average of the same species in five areas sampled by Beaton *et al.* (1965). On an air dry basis the protein was approximately 7.75 per cent which is greater than the 4.52 per cent (air dry) average protein content reported by Boag and Kiceniuk (1968) for lodgepole pine in southwestern Alberta. Gross energy is high in pine needles (5.32 Kcal/g) when compared to the commercial turkey ration (4.68 Kcal/g) fed captive spruce grouse. The values found are in general agreement with those of other workers (Boag and Kiceniuk, 1968). Much of the gross energy value, however, would be contributed by crude fiber for which the digestibility is low and consequently these values do not give much indication of the energy value of the needles for the bird. The levels of the mineral elements other than sodium and phosphorus are similar to the values found by Beaton *et al.* (1965).

Calcium level was higher in old spruce needles than in pine needles (0.43% vs. 0.10%). It is noteworthy that in the early spring when requirements for calcium would be greater because of reproduction, the females consumption of spruce needles increased, although the change was not statistically significant. In late June the females may have a high requirement for protein or specific amino

acids, needed to replenish losses during laying and incubation, this would be provided by the new spruce growth taken at that time in significant quantities.

Although too few analyses were done on foods other than pine needles to allow statistical comparison of nutrients, the differences were great in some cases.

Bilberry leaves and moss sporophytes utilized in summer were higher in protein but lower in caloric value than conifer needles. The crude fiber content was lower than in pine needles, indicating that the available food energy may be as great or greater than in the winter diet. Calcium was low in moss sporophytes but high in bilberry leaves when compared to the winter food. Levels of potassium and sodium in these foods were in the same general range as they were in the winter diet.

Bilberries were higher in protein than pine needles but cranberries were not. It is possible that the amino acids of cranberries may complement those of pine needles and other foods, but no analyses of amino acid content of cranberries were done. Caloric values were lower in both these berries than in conifer needles, but as in leaves the level of crude fiber was also lower, indicating a greater potential food utilization as found by Pullaininen *et al.* (1968) for cranberries in willow grouse. The level of minerals in the two berries was very similar to that of conifer needles, except for a high level of phosphorus in bilberries. The phosphorus of bilberries may be

important to growing birds.

Other summer foods, sedge seeds, bilberry flowers, twisted stalk and horsetail were all richer in protein but lower in caloric value than pine needles.

The level of the minerals; calcium, phosphorus, and sodium of all foods analysed were low when compared to the requirements of domestic chickens, as given by the National Research Council's Nutrient Requirements of Poultry (1966) (calcium - 2.25% and 1.0%, phosphorus - 0.6% and 0.6%, sodium - 0.15% and 0.15% for laying hens and growing chicks respectively). The requirements of laying domestic hens, probably are not directly comparable to those of laying spruce grouse as spruce grouse produce only 4-7 eggs (Godfrey, 1966). Furthermore, the rate of egg production in captive female spruce grouse was approximately one egg in two days which is similar to the rate in wild birds of 4 eggs in 6 days observed by McCourt (pers. comm.) which is lower than in domestic chickens.

It has been postulated that grouse select between needles of different trees of the same species (Seiskari, 1962) and between needles of different quality in different areas on the same tree (Hoffman, 1961). In this study there was selection between needles of different species and between old and new growth of spruce. New growth of spruce utilized was obviously different in appearance from the needles produced the previous year. With this one exception there was no evidence that the birds could

detect needles containing different nutrient levels on the same tree or between different trees.

4. Digestion of pine needles by spruce grouse

The nutrient content of food items has little meaning unless combined with digestibility studies to determine the availability of nutrients to the animal. The amount of a nutrient which is absorbed is a function of total food intake, which in turn is largely determined by the available energy in the food (Hill and Dansky, 1954). This energy, known as metabolizable energy, is the difference between caloric value of food multiplied by the weight consumed in a given time, minus caloric value of feces and urine produced multiplied by their weight.

Metabolizable energy (M.E.) of pine needles was calculated from the data of Tables 7 and 8, to facilitate determination of nutrients available in this food for spruce grouse. The first method is based on total mass of food consumed and feces eliminated (Maynard and Loosli, 1962).

$$\text{Per cent M.E.} = \frac{100 (ac - bd)}{ac}$$

a = caloric value of food

b = caloric value of feces

c = dry weight of food

d = dry weight of feces and urine

Table 7. Rates of pine needle consumption and feces elimination by six captive spruce grouse.

Mean dry weight in grams per day for 51.4 days

Needles consumed	Caecal feces	Intestinal feces	Total feces	Food absorbed
40.4	2.2	27.3	29.5	10.9

Table 8. Analyses of food and feces of captive spruce grouse when on a pine needle diet.

	Kcal/g	% protein	% crude fiber	% lignin
Pine needles (N=5)				
mean	5.24	8.36	39.62	21.05
std. dev.	0.03	1.52	1.72	2.07
Caecal feces (N=9)				
mean	5.58	20.84	19.48	13.74
std. dev.	0.04	2.36	6.12	5.91
Intestinal feces (N=11)				
mean	5.00	14.33	53.02	29.78
std. dev.	0.1	1.05	4.78	3.33
*Average of caecal and intestinal feces	5.04	14.80	50.98	28.59

*Weighted to correspond to the proportion of the two types of foods produced (from Table 7).

Using the data from Tables 7 and 8 the metabolizable energy was calculated as follows:

$$\text{M.E.} = 100 \times \frac{5.24 \times 40.4 - 5.04 \times 29.5}{5.24 \times 40.4} = 29.8\%$$

A second method is based on the principle that an indigestible and unabsorbable substance in the food can be used as a digestibility marker (Forbes and Garrigus, 1948). This method uses lignin as a "marker".

$$\text{Per cent M.E.} = 100 - 100 \left(\frac{e}{f} \times \frac{b}{a} \right)$$

a = caloric value of food

b = caloric value of feces

c = per cent lignin in food

f = per cent lignin in feces

Using the data from Tables 7 and 8 the metabolizable energy was calculated as follows:

$$\text{M.E.} = 100 - 100 \left(\frac{21.05}{28.59} \times \frac{5.04}{5.24} \right) = 29.2\%$$

The results of these two calculations are similar and correspond closely to the digestibility of blueberry stems by willow grouse (*Lagopus lagopus*) of 31 per cent (Pullianinen *et al.*, 1968), indicating that both foods are of low digestibility.

In order to compare the pine needle diet with commercial diets for domestic fowl, data were manipulated to correspond to units used by poultry nutritionists. Energy in feeds is usually expressed as metabolizable energy per pound. This value calculated for pine needles is 706 Kcal per pound (per cent metabolizable energy x caloric value

of food x grams per pound). Domestic chickens can be maintained and even grown on rations as low as approximately 720 Kcal per pound of metabolizable energy (Hill and Dansky, 1954). The amount of energy taken in per day depends on the metabolizable energy of the food and the amount consumed. The total amount of energy assimilated by grouse per day can be calculated from the following formula.

$$\text{Energy intake} = a \times c \times \frac{\text{per cent M.E.}}{100}$$

a = caloric value of food

c = dry weight of food consumed per day

Using the data from Tables 7 and 8 the daily energy consumption of captive birds was calculated as follows:

$$\text{Energy intake} = 5.24 \times 40.4 \times \frac{29.8}{100} = 63 \text{ Kcal per day}$$

While McDonald *et al.* (1966) state that a domestic chicken of 575 grams would require approximately 79 Kcal per day for normal activities, Brody (1964) states that a bird of this size would require 60 Kcal per day for its basal metabolism. The somewhat low value for grouse may have been made up by drawing on protein reserves resulting in the negative nitrogen balance discussed later.

Under normal conditions animals eat to meet their energy requirement (Hill and Dansky, 1954). For this reason the amount of protein consumed is related to the digestible energy of food as well as the simple percentage of protein in food. For these reasons metabolizable energy

per one per cent protein (c/p ratio) is of importance in formulating rations for domestic stock. The c/p ratio of pine needles is 83.5 which is comparable to rations fed domestic poultry for finishing as well as laying (Morgan and Lewis, 1962). The ratio required for simple maintenance would probably be greater than this figure and, as discussed in section 3, because grouse produce eggs at a much lower rate than domestic chickens, their laying requirements would not be as great as domestic chickens.

Captive birds appeared to vary in their ability to digest needles. Calculations of apparent digestibility of protein by birds includes the protein (actually mainly uric acid) excreted by the kidneys and incorporated into the feces. In a bird which is maintaining its weight the protein taken in equals that deaminated and excreted so that the apparent digestibility of protein is near 0. Table 9 shows that on the average, birds lost weight during the digestibility experiments. This weight loss is reflected in a greater quantity of protein in the feces than in the food (a negative nitrogen balance). Table 7 shows that the average daily consumption of pine needles was 40.4 grams per bird. Of this quantity 8.36 per cent (Table 8) or 3.4 grams was protein. In the feces produced per day, 29.5 grams contained 14.7 per cent or 4.3 grams of protein. The birds were therefore losing approximately one gram of body protein per day. Table 9 shows that this loss, however, varied greatly from bird to bird. The birds

Table 9. Weight changes in captive birds while on pine needle diets from January through March, 1968.

1. Birds used in digestibility studies which had been on an artificial diet for more than 3 months.

Number of birds	Days on needle diet	Original weight in grams		Daily weight change in grams	
		Mean	Range	Mean	Range
3	5-7	632	590-663	-5.4	-11- -2.5

2. Birds used in digestibility studies which had been recently captured.

Number of birds	Days on needle diet	Original weight in grams		Daily weight change in grams	
		Mean	Range	Mean	Range
3	7-14	560	507-590	-1.7	-10.3- +9.6

3. All birds used in digestibility studies.

Number of birds	Days on needle diet	Original weight in grams		Daily weight change in grams	
		Mean	Range	Mean	Range
6	5-14	592	407-663	-2.8	-11- +9.6

4. Birds not used in digestibility studies which had recently been captured.

Number of birds	Days on needle diet	Original weight in grams		Daily weight change in grams	
		Mean	Range	Mean	Range
2	61	559	545-573	+1	+0.07- +0.13

were of two types. The group showing a high weight loss on the needle diet had been in captivity since summer and maintained on artificial foods. The group showing little weight loss and in some cases a weight gain on the needle diet had been captured immediately before the experiments. It appears that the gut tract may be conditioned to specific diets. Further evidence of this adaptation is discussed later.

Proteins are needed primarily as sources of amino acids (Morgan and Lewis, 1962). These authors give the following formula from which the maintenance and laying requirements for amino acids can be calculated:

$$\text{Percentage of methionine required in ration} = \frac{C(0.05W \pm 6.2\Delta W + 5E)}{453 \uparrow (1.52W \pm 0.653 \pm 3.26\Delta W + 3.29E)}$$

where C = Kcal of metabolizable energy per pound
of ration

W = average body weight per hen in grams

ΔW = average daily change in body weight per
hen in grams

E = average weight in grams of eggs produced
per hen per day

$\uparrow$ = 1 in spring (temperature correction factor
for each season)

The following conversion factors are multiplied by the calculated methionine requirement to obtain the estimated needs for the other essential amino acids: methionine 1.0, methionine + cystine 1.7; histidine 0.73; isoleucine 2.09;

leucine 2.85; lysine 2.09; phenylalanine plus tyrosine 3.0; tryptophan 0.49; threonine 1.52; and valine 2.24. For maintenance (weight change and egg production equal to 0) the requirements for methionine can be calculated as follows for a 513 gram female.

$$\begin{array}{l} \text{Percentage of} \\ \text{methionine} \\ \text{required in} \\ \text{ration} \end{array} = \frac{706(0.05 \times 513 \pm 6.2 \times 0 + 5 \times 0)}{4537 \times 1(1.52 \times 0^{0.653} \pm 3.26 \times 0 + 3.29 \times 0)} = .05\%$$

For a female laying 9.5 grams of eggs and losing 2.7 grams of body weight per day (based on egg weight, rate of laying and weight loss of females in the laying season from Figure 2) the requirement was calculated as follows.

$$\begin{array}{l} \text{Percentage} \\ \text{methionine} \\ \text{required} \\ \text{in ration} \end{array} = \frac{706(0.05 \times 567 + 6.2 \times -2.7 \times 5 \times 9.5)}{4537 \times 1(1.52 \times 2.7^{0.653} + 3.26 \times -2.7 + 3.29 \times 9.5)} = .08\%$$

The c/p ratios used for comparison with domestic chickens assume adequate ratios of amino acids to energy. The amino acids present in pine needles and requirements calculated as shown above are presented in Table 10. Tryptophan and cystine are destroyed by the method of hydrolysis used therefore cannot be considered. The total amino acids analysed equals 5.54 per cent. The crude protein ($X \times 6.25$) for the needles analysed for amino acids was 7.25 per cent.

Assuming that the amino acid requirements of domestic chickens is not vastly different from that of grouse, Table 10 shows that all amino acids with the possible exception of methionine are present in adequate quantities

Table 10. A comparison of amino acids present in pine needles and requirements of grouse based on a formula derived for domestic poultry (from Morgan and Lewis, 1962). All requirements are based on a diet of 706 Kcal M.E./lb.

	Per cent dry weight	Maintenance requirement	Laying requirement
Lysine	.37	.10	.16
Histidine	.08	.04	.06
Threonine	.07	.07	.12
Valine	.43	.10	.18
Methionine	.04	.05	.08
Methionine+ Cystine	cystine destroyed	.07	.13
Isoleucine	.35	.10	.16
Leucine	.56	.13	.22
Tyrosine	.18	.14	.25
Phenylalanine	.36		
Tryptophan	destroyed	.02	.03
Arginine	.38	-	-
Glycine	.37	-	-
Alanine	.41	-	-
Aspartic acid	.63	-	-
Serine	.28	-	-
Glutamic acid	.73	-	-
Proline	.30	-	-
Total	5.54	-	-

in pine needles for maintenance and laying. In support of the contention that pine needles have adequate amino acids for maintenance two grouse were maintained in satisfactory condition in captivity for two months (Table 9) on a diet only of pine needles with access to soil for possible grit and mineral needs. In the wild, females did not produce eggs on a diet solely of pine needles but utilized spruce needles and bog cranberries before and during laying. Since amino acid analyses were not done for these foods it cannot be assumed that the methionine level of the diet taken as a whole was low.

The low digestibility of the energy components of pine needles requires that an animal feeding on them be able to consume large quantities to obtain sufficient energy. Because of the high consumption rate, other nutrients in the food, such as protein and minerals, would be consumed in greater quantities than their percentage of the food appears to indicate. Thus, the low percentage of some nutrients in pine needles does not necessarily mean that an animal consuming them will suffer from deficiencies.

5. Condition of adult birds over the year

One means of evaluating the quality of an animal's diet is to examine its state of health (i.e., condition). Robel and Linderman (1966) suggest that total weight changes of birds could reflect availability and/or energy content of food. Bump *et al.* (1949) state that body

weight is a good index of condition in ruffed grouse. To give an indication of condition of spruce grouse comprising the monthly samples Figures 2, 3, 4, and 5 show average total body weight, weight of pectoralis major, pectoralis minor, heart, and liver. The differences between winter (November to April) and summer (May to October) conditions as reflected in weights and measurements were tested for significance.

Both males and females were heavier in winter than in summer, though the difference was not statistically significant based on 6-month winter and summer periods. The weights of females increased a highly significant amount in May. At this time average weight of females surpassed that of males. This phenomenon was noted by Lewin (1963) in California quail (*Lophortyx californicus*). He attributed this increase in weight to hypertrophy of reproductive organs. In spruce grouse there was also an increase in fat deposition, a highly significant increase in liver weight and a significant increase in pectoralis muscle weight. This situation agreed with that found in female pheasants by Kirkpatrick (1944), who found that gonad weight alone could not account for the increase in weight before laying. It is noteworthy that these increases occurred in spruce grouse when the diet consisted mainly of conifer needles with some cranberries. Therefore, it would appear that these foods are more than adequate for maintenance of body condition and general health.

Figure 2. Mean total weights of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 3. Mean weights of *pectoralis major* and *pectoralis minor* muscles of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

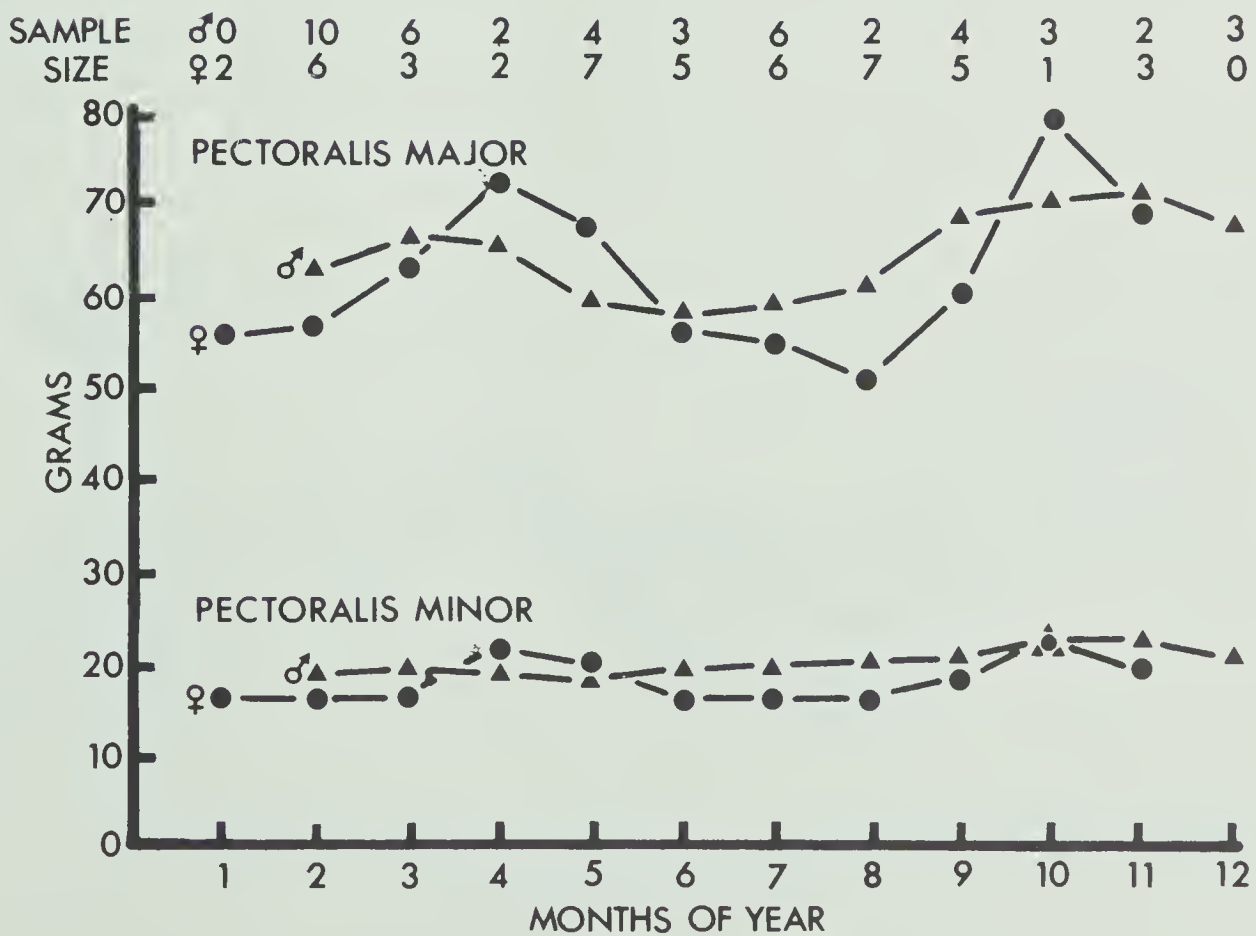
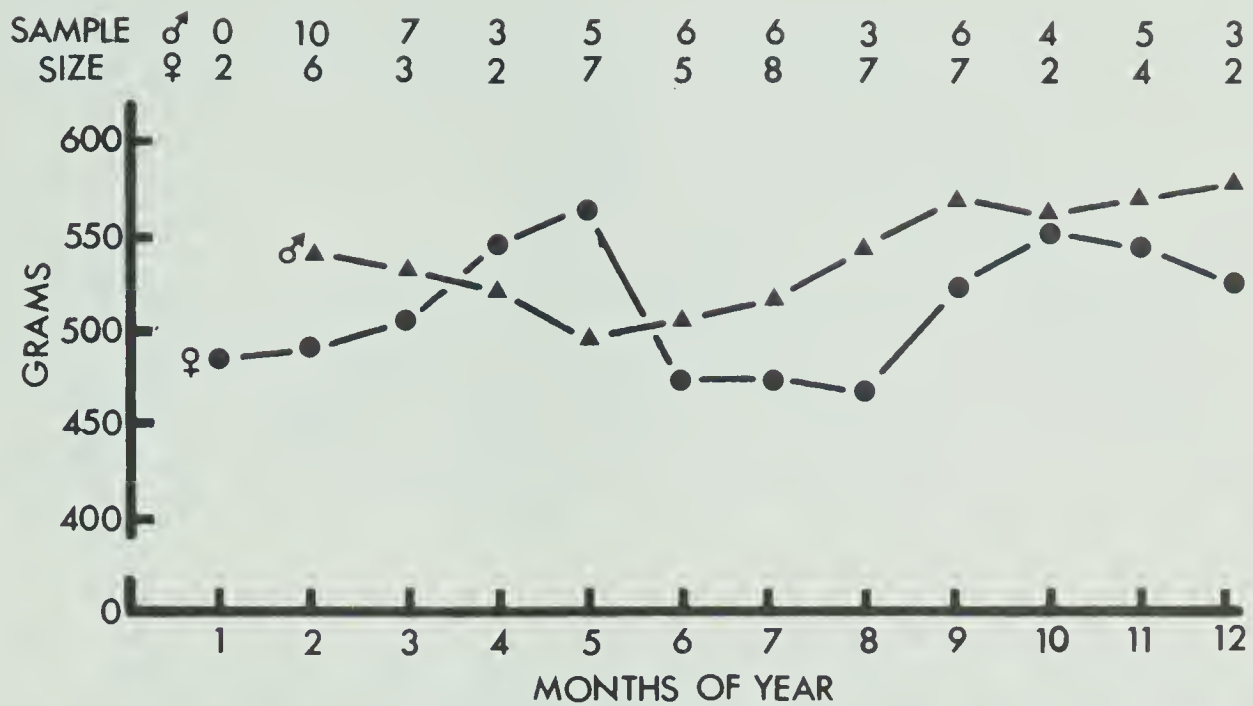
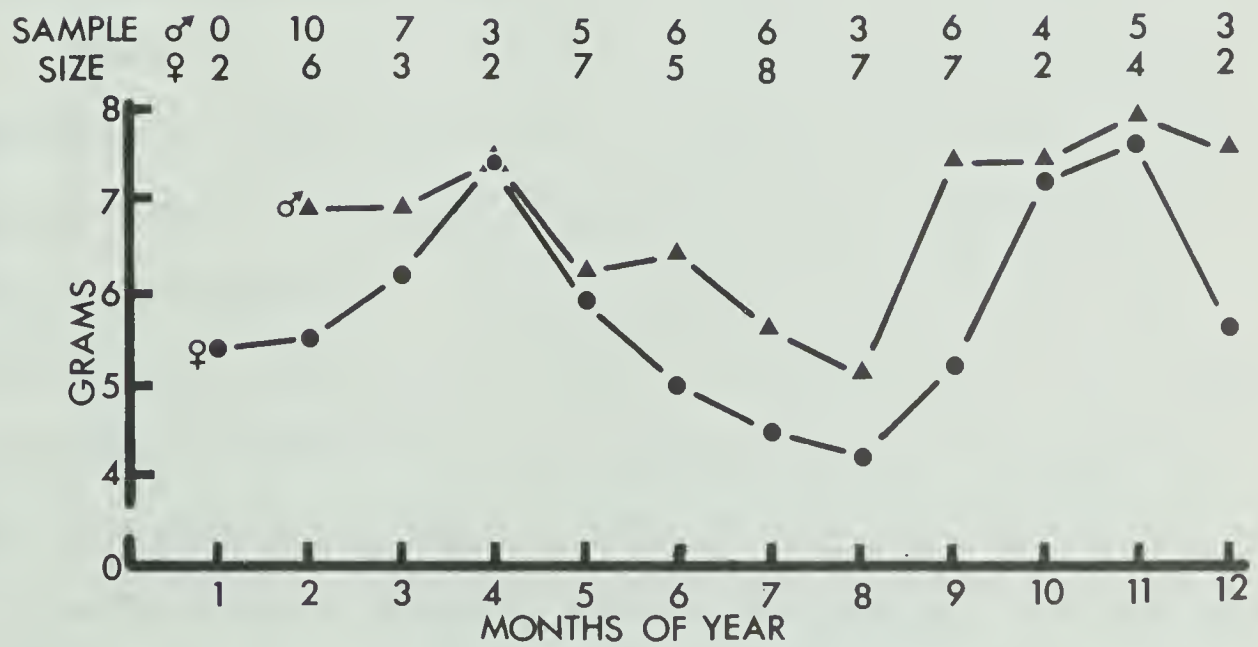
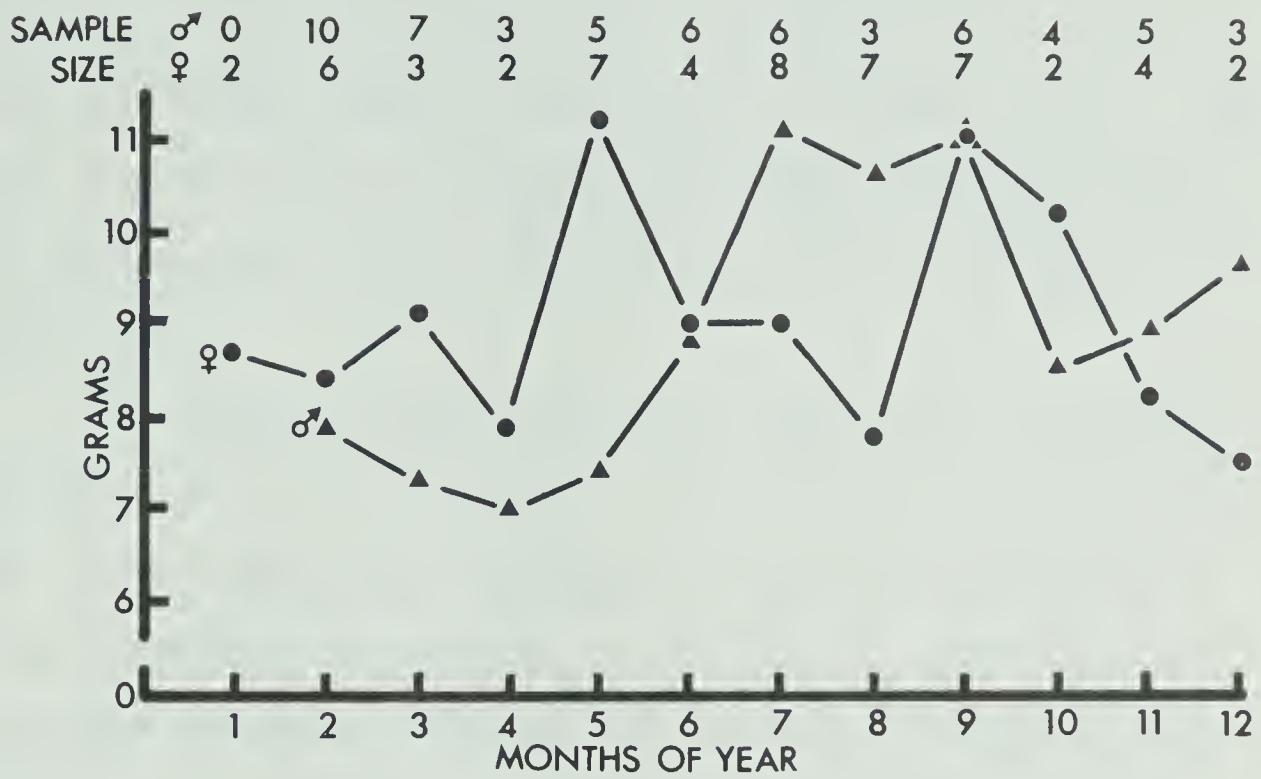


Figure 4. Mean weights of livers of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 5. Mean weights of hearts of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.



Neither males nor females showed any significant difference between summer and winter weights of the pectoralis muscles (Figure 3). Starving birds quickly mobilize these muscles resulting in a weight loss. That this did not occur indicates that those spruce grouse collected were able to meet their food requirements in the winter.

The weight of the hearts of both sexes increased significantly in the winter. Two factors could account for this. Firstly, the digestive system increased in size in winter (discussed in Section 7) requiring circulation of blood through more tissue. Secondly, an increase in metabolism in winter as shown by Delane (1968) in pheasants and Hungarian partridges, may require a more rapid circulation; and therefore a larger heart. Also, Bump *et al.* (1947) showed that the heart rate increased with decreased environmental temperature in ruffed grouse.

The liver was the only organ showing a significant decrease in weight in winter. Weights of livers of male spruce grouse increased from May to June and remained high until November, corresponding to the period when berries and leaves were abundant in the diet. As already mentioned, weights of livers from females collected in May were high but dropped during incubation and moult to an overall low in August, which corresponds to a minimum total weight in the same month. In September, a time when females are released from brood care and can feed

independently on the abundant fruit available, the liver weight increased to the same level as that of males and like the males remained high until winter.

During the year in which spruce grouse were studied, the reproductive cycle appeared to have a greater impact on body condition than did the environmental factors of winter food and weather. Thus, the winter diet could not have been marginal for maintenance.

6. Physiology of digestion

Crude fiber digestion

The caeca of all tetraonids are very large and together usually approach the weight of the small intestine (Leopold, 1953). Many people have assumed that because the tetraonids, as a whole, utilize foods high in crude fiber, that these organs must somehow be connected with crude fiber breakdown (Suomalainen and Arhimo, 1945; McBee and West, 1969). Using lignin as a marker the digestibility of crude fiber in needles entering and by-passing the caeca were calculated using the following formula:

$$\text{Digestibility} = 100 - \left(100 \times \frac{e}{f} \times \frac{g}{h} \right)$$

e = per cent marker in food

f = per cent marker in feces

g = per cent crude fiber in feces

h = per cent crude fiber in food

Using the data in Table 8, the digestibility of crude fiber was calculated as follows:

Digestibility of crude fiber in food entering the

$$\text{caeca} = 100 - \left(100 \times \frac{21.05}{13.74} \times \frac{19.48}{39.62} \right) = 24.8\%$$

Digestibility of crude fiber in food not entering

$$\text{the caeca} = 100 - \left(100 \times \frac{21.05}{29.78} \times \frac{53.02}{39.62} \right) = 5.4\%$$

Since the food entering the caeca also passed through the rest of the gut tract the crude fiber actually broken down in the caeca would be only $24.8 - 5.4 = 19.4\%$. As lignin in plant cells, and most other carbohydrates of the crude fiber complex are found mainly in the cell walls (Ewing, 1949), they can be assumed to enter the caeca in approximately the same proportions relative to each other, as found in the food.

$$\begin{aligned} &\text{Lignin entering the caeca} = \text{percentage of feces} \\ &\text{from the caeca} \times \frac{\text{lignin in caecal feces}}{\text{lignin in all feces}} \end{aligned}$$

Using the data from Tables 7 and 8 the lignin and crude fiber entering the caeca = $100 \times \frac{2.2}{29.5} \times \frac{13.74}{28.59} = 3.6\%$.

Crude fiber digested by the caeca is the product of crude fiber entering the caeca and digestibility of crude fiber in the caeca = $\frac{19.4 \times 3.6}{100} = 0.69\%$

Even allowing considerable error in this method of calculating crude fiber digestion, it appears that though this digestion does occur in the caeca, it is of too small a quantity to be of any significance to the birds. As Pullianinen *et al.* (1968) state, the anatomical hint

that the main function of the caeca is for crude fiber digestion is not dependable.

Utilization of high fiber foods

Nitrogen content and caloric value of caecal feces are higher than that of either ingested food (pine needles) or intestinal feces (Table 8). Small amounts of lignin in caecal feces indicate that caecal contents are derived largely from the protoplast of cells which is probably higher in protein than cell walls. This separation of fibrous material and protoplast is probably accomplished by the ventriculus. Table 11 shows a drop in fiber content in the anterior small intestine and an increase in nitrogen content indicating that the ventriculus squeezes the liquid from the needles into the intestine during maceration. Imondi and Bird (1965) found a similar rise in nitrogen concentration in the duodenum of chickens. Such a separation of food constituents may allow more efficient utilization of digestive enzymes by concentrating digestion on cell contents. Fibrous material, which is largely indigestible, may be held in the ventriculus and then passed through the intestine quickly.

Table 11 shows that many nutrients are in higher concentrations in the gut tract than in pine needles. The separation of fibrous from liquid parts of the food may be one factor involved. Factors affecting mineral concentration are the varying quantities of grit and soil eaten

Table 11. Analysis of gut tract contents of spruce grouse collected during the part of the year when pine needles comprise the sole food in the Swan Hills, Alberta.

	Kcal/g	per cent moisture	per cent protein	per cent crude fiber	per cent lignin	per cent calcium	per cent phosphorus	per cent magnesium	per cent potassium	per cent sodium
Crop contents (N=7)										
mean	5.33	0.1	9.0	56.6	31.1	.03	.13	.10	.52	.22
std. dev.	.09	7.2	.6	24.3	3.6	.03	.03	.02	.11	.05
Anterior small intestine contents (N=6)										
mean	5.48	8.7	35.8	23.4	11.4	.12	.61	.10	1.54	1.60
std. dev.	.18	2.7	1.1	2.7	3.0	.08	.08	.00	.15	.19
Posterior small intestine contents (N=9)										
mean	5.35	7.1	22.8	49.1	19.1	.06	.34	.06	1.24	1.02
std. dev.	.13	1.8	3.1	-	1.9	.03	.15	.03	.46	.42
Caeca contents (N=8)										
mean	5.50	7.7	36.6	31.5	26.8	.09	.79	.19	2.36	.44
std. dev.	.38	.8	1.5	8.4	7.8	.19	.26	.06	.76	.12
Large intestine contents (N=4)										
mean	5.11	5.9	12.2	47.9	28.2	.11	.35	.13	1.82	.19
std. dev.	.10	1.0	2.2	3.7	7.4	.03	.04	.00	.15	.11

by the birds and the excretion of some minerals by the gut tract (Mueller, 1956). These factors would not account for the high level of nitrogen in the posterior part of the gut tract as most of the protein eaten by domestic fowl is absorbed in the anterior jujenum (Imondi and Bird, 1965). The intestines and their contents were preserved by freezing which may have caused a breakdown of the gut tract lining and its adherence to the food. The gut tract lining added to the contents removed would increase the percentage of protein shown in the analyses.

It was considered impossible to trace the absorption of nutrients using this data because of the factors described above.

7. Seasonal adaptations of the gut tract

Leopold (1953) observed that gallinaceous birds utilizing leafy foods with high roughage have larger digestive systems than those feeding on seeds, and that populations of California quail in different areas and utilizing different types of food had different sized intestines, caeca, and stomachs. Lewin (1963) found in a population of California quail, that in a change from a summer diet of seeds to a winter diet of leafy material, there was an increase in weight of ventriculus, in weights and lengths of small intestine and caeca, and in length of villi of the small intestine, though there was little change in the large intestine.

The average monthly weights and lengths of measured internal organs of grouse collected over the year are shown in Figures 6, 7, 8, 9, 10, 11, 12, 13, 14, and 15.

The data for each sex were lumped from May through October (summer) and November through April (winter) and the differences tested for significance. Although there were no significant differences in total weight or in the muscles weighed for these times (section 5), the following measurements of organs were highly significantly greater in the winter in both sexes: weight of empty proventriculus, weight of empty ventriculus, weight of empty large intestine with cloaca, weight of full caecum, weight of pancreas, length of caeca and length of large intestine with cloaca. The small intestine weights and lengths averaged slightly more in the winter than in the summer period but the difference was not significant.

The changes in the gut tract were not caused by the same factors as the seasonal hypertrophy and atrophy of reproductive organs, since the gut tract changes of captive birds fed a concentrated diet did not correspond to the changes in the wild birds (Table 12), even though the time of breeding was similar. Furthermore, Lewin (pers. comm.) found that in California quail the gut tract could be stimulated to change from a "summer size" to a "winter size" within two weeks of a change in diet from seeds to leafy foods. For these reasons it seems likely that the changes in the gut tract result from stimulation by the foods themselves.

Figure 6. Mean lengths of small intestines of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 7. Mean lengths of caeca of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

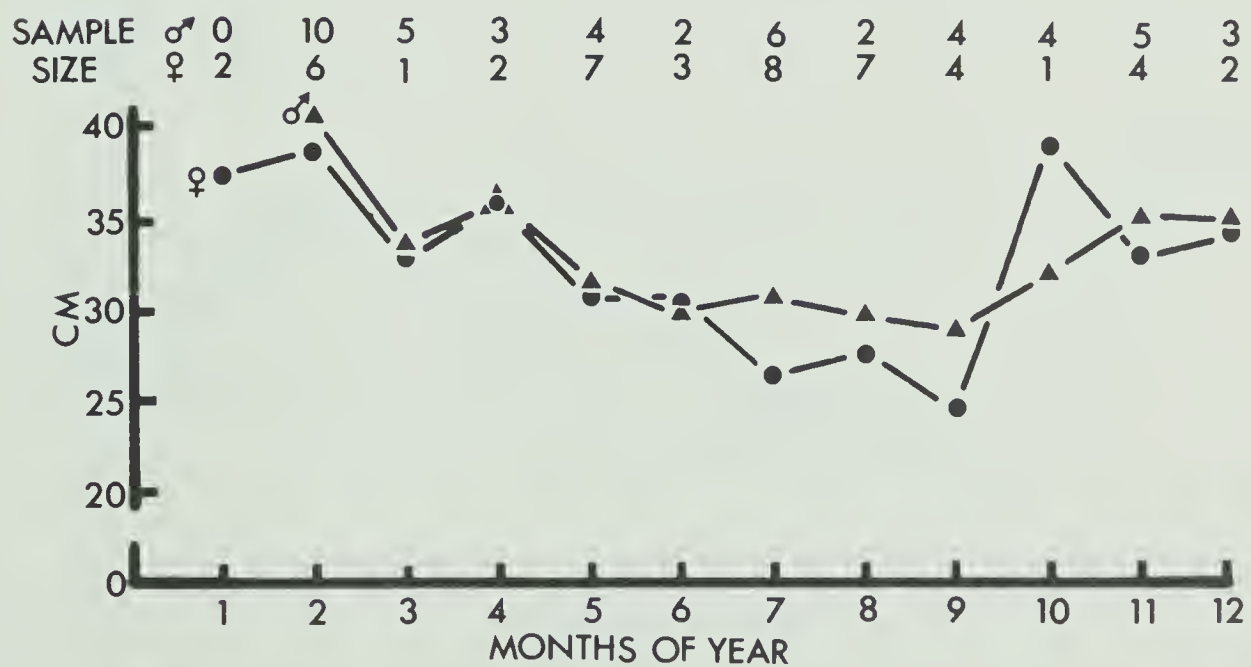
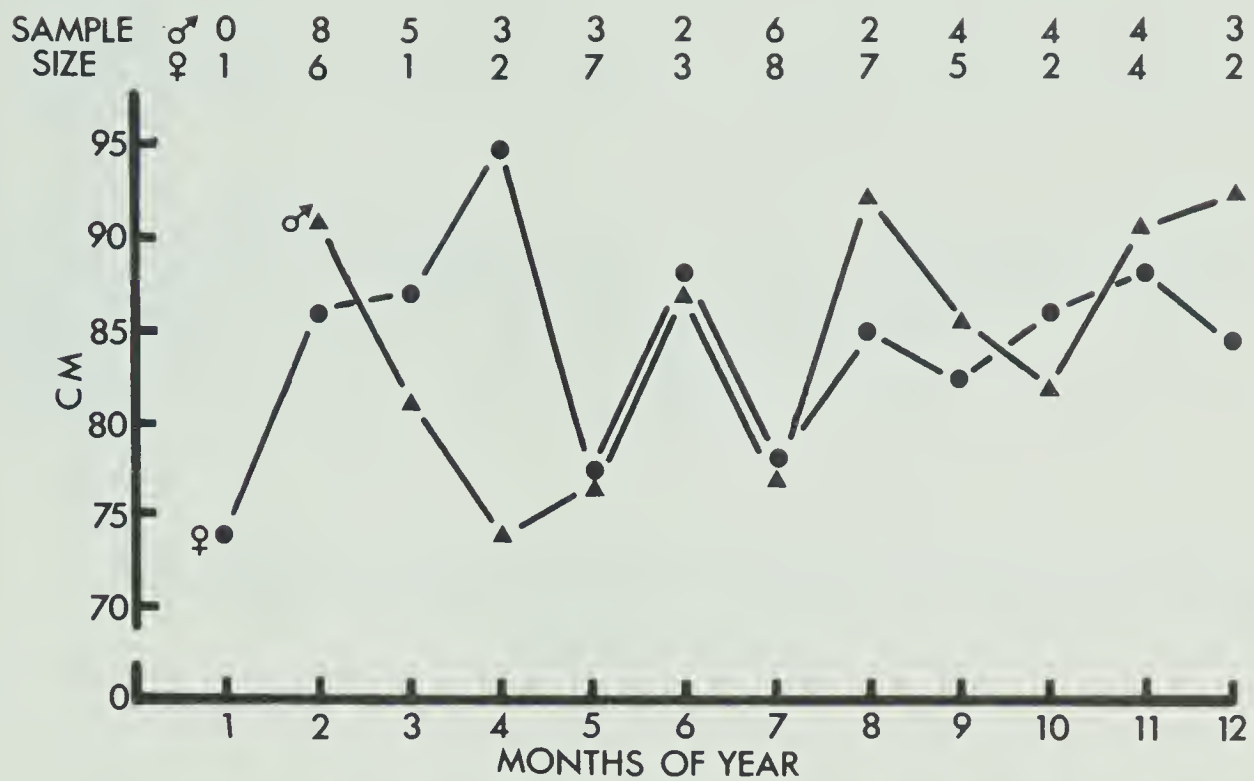


Figure 8. Mean weights of pancreas, of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 9. Mean lengths of large intestines and cloacas of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

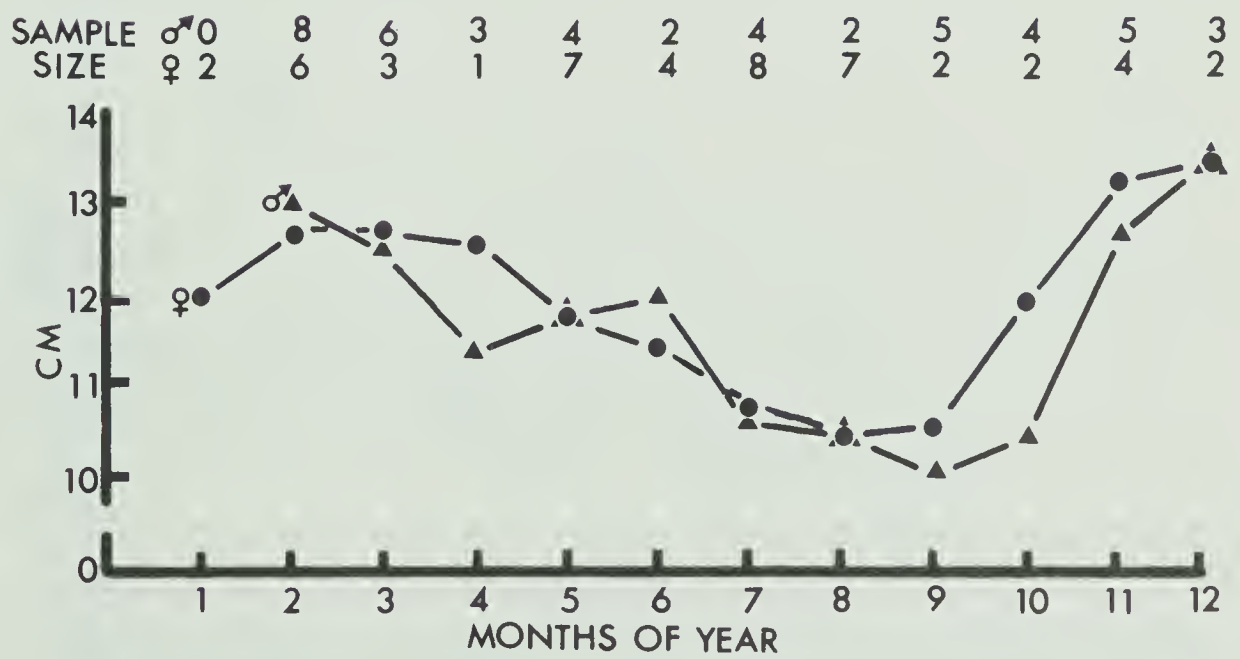
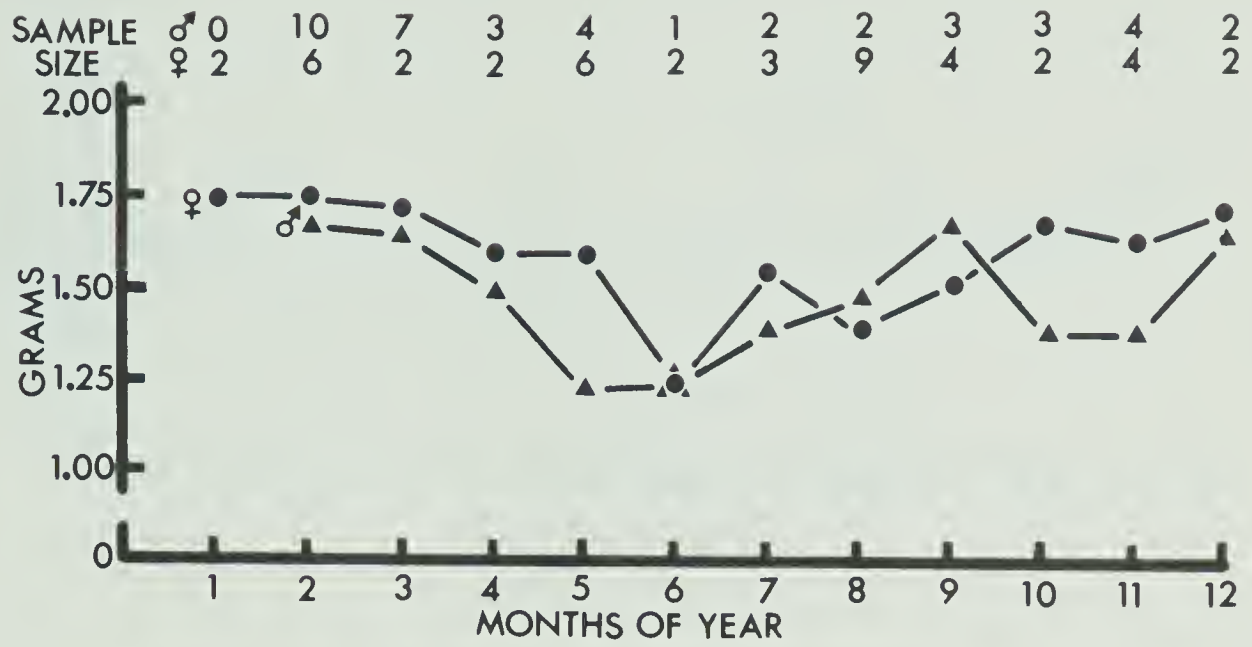


Figure 10. Mean weights of full small intestines of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 11. Mean weights of full caeca of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

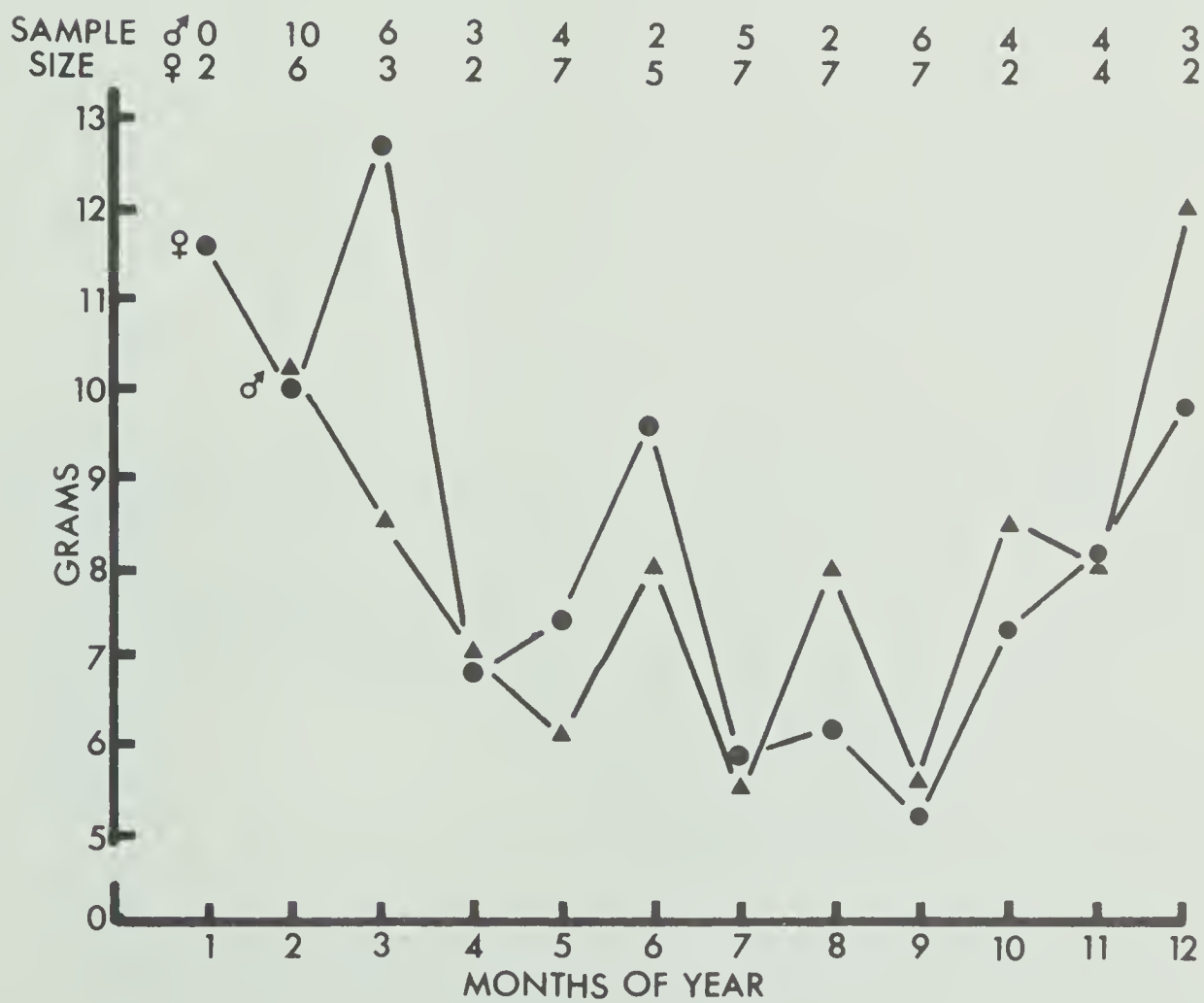
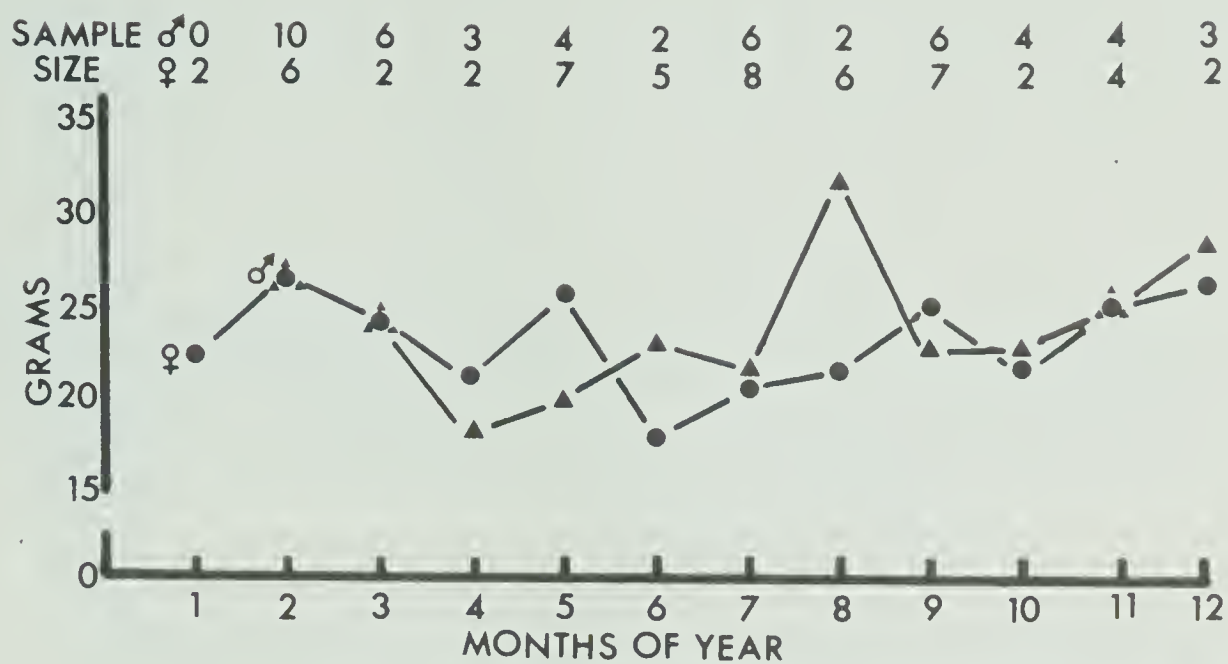


Figure 12. Mean weights of empty proventriculi of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 13. Mean weights of empty ventriculi of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

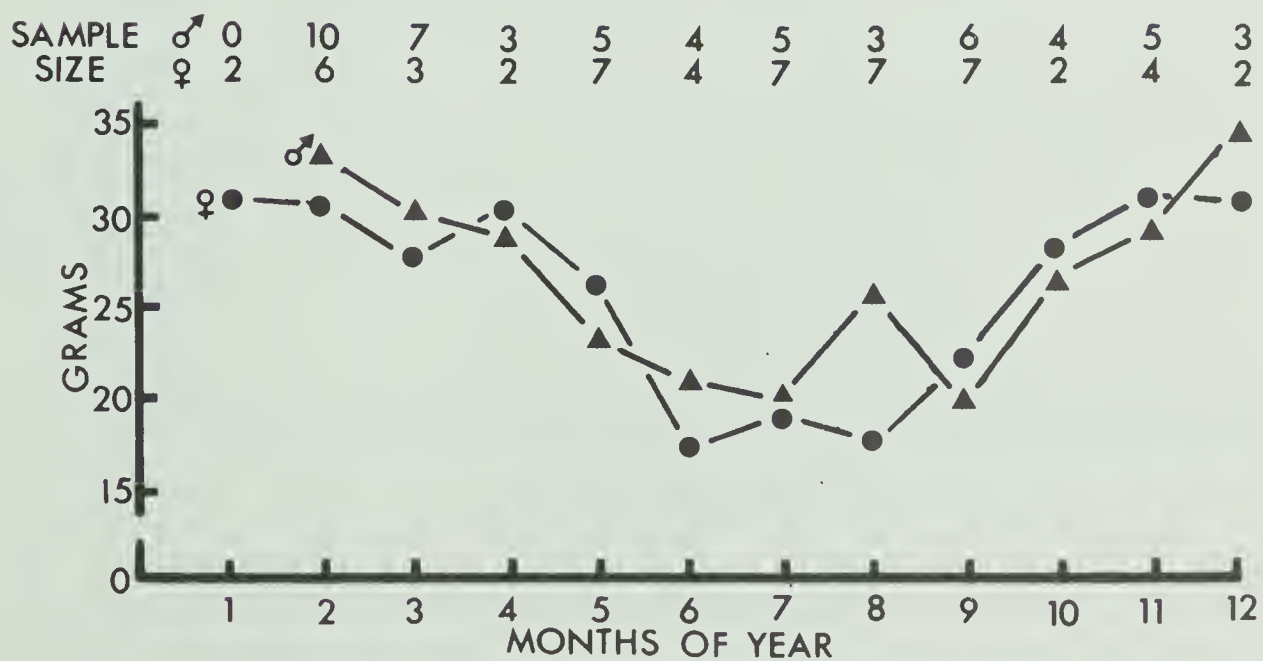
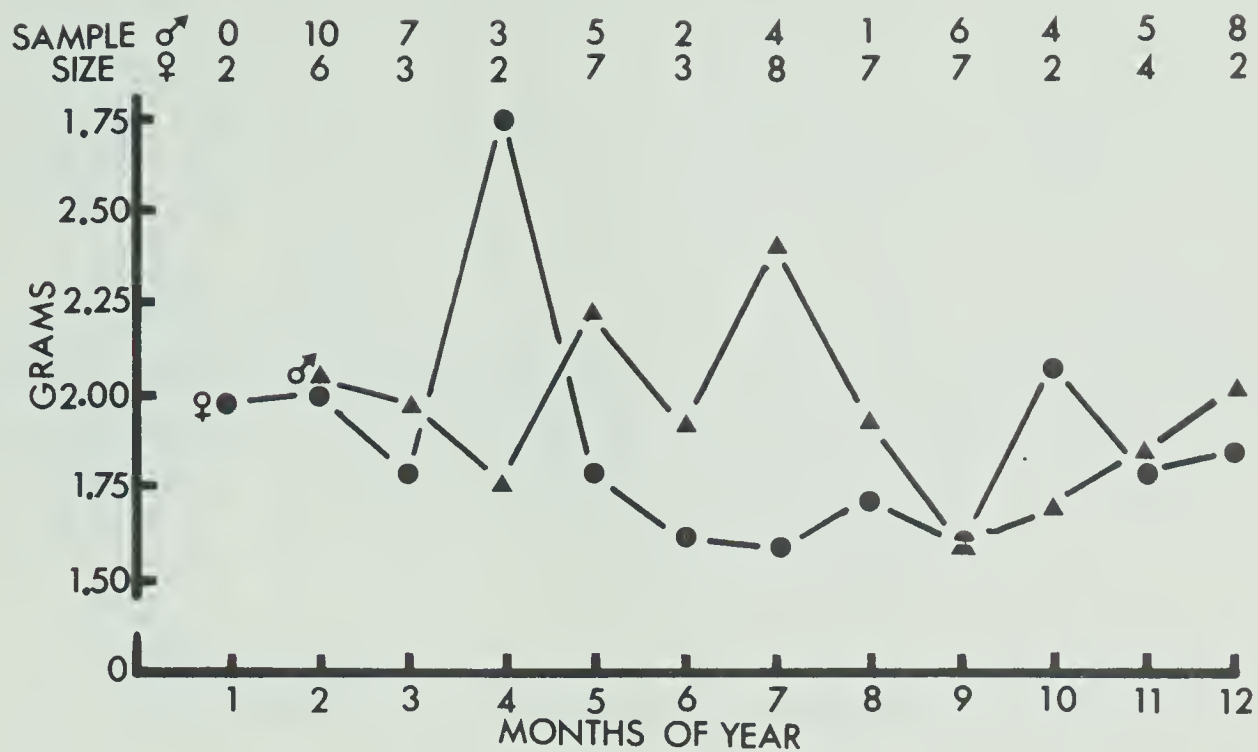


Figure 14. Mean weights of empty crops of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

Figure 15. Mean weights of empty large intestines and cloacas of adult spruce grouse collected on a monthly basis throughout the year from the Swan Hills, Alberta.

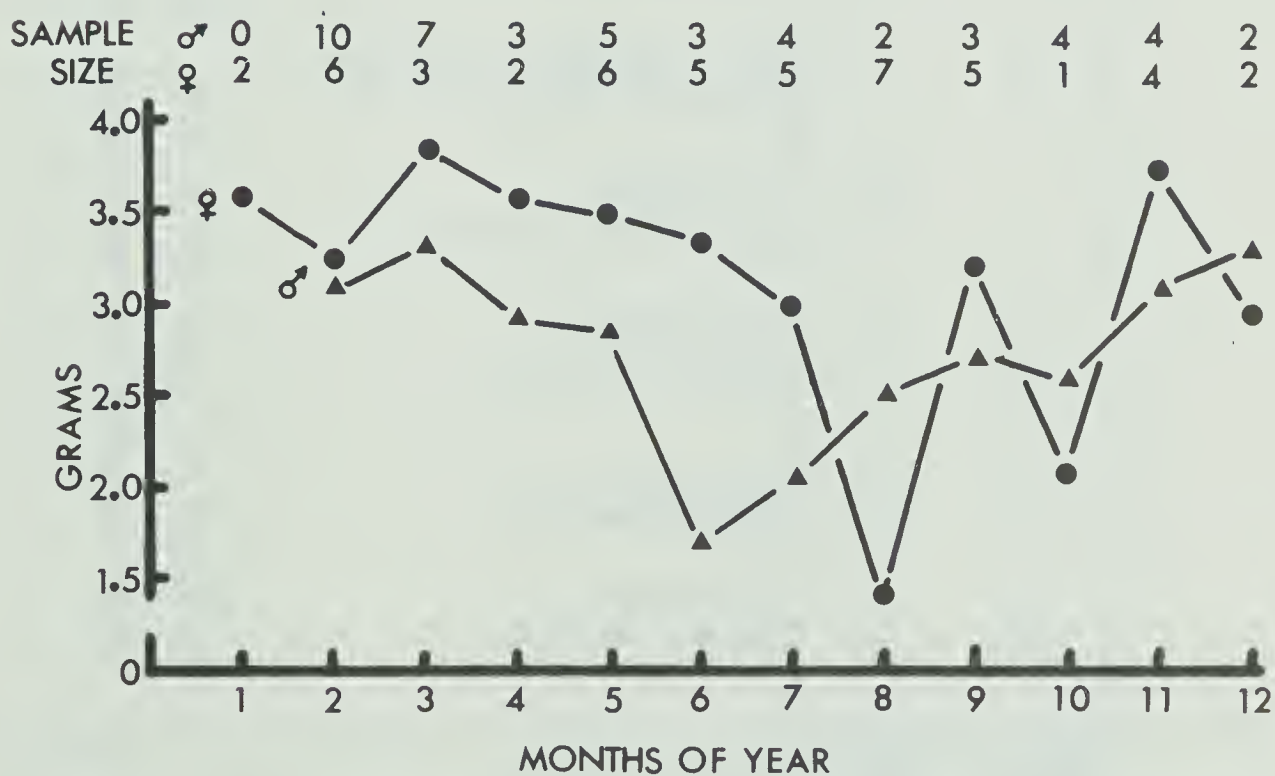
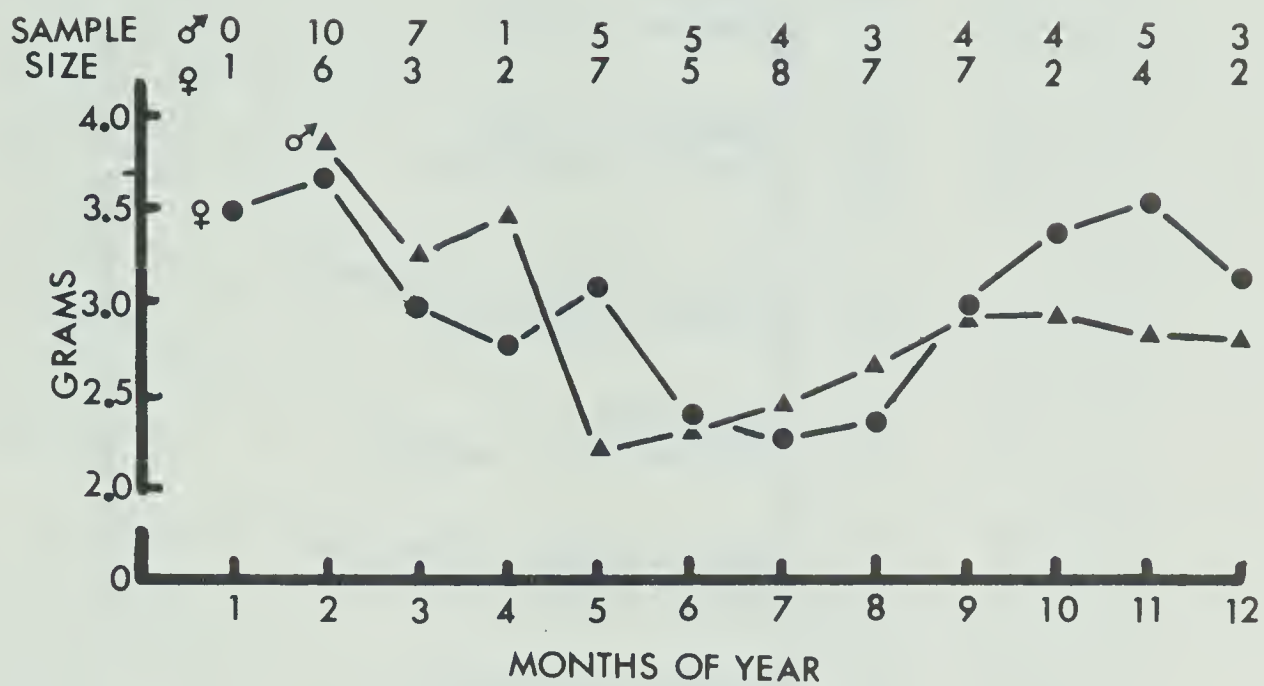


Table 12. Measurements of captive birds killed in winter after feeding on an artificial diet more than four months.

Number	Date killed	Total weight in grams	Heart weight in grams	Liver weight in grams	Pancreas weight in grams	Proventriculus full weight in grams	Ventriculus full weight in grams	Ventriculus empty weight in grams	Small intestine full weight in grams	Caecum full weight in grams	Large intestine full weight in grams	Small intestine length in cm.	Caecum length in cm.	Large intestine length in cm.
1	Feb. 24 1968	617	8.89	19.4	1.80	2.3	28.2	20.8	17.1	4.9	9.2	90.0	27.0	9.2
2	April 16 1968	607	9.37	23.0	-	1.9	25.2	18.5	13.4	4.0	-	76.0	22.0	9.0

Two factors may account for the need of a general increase in size of the digestive system in winter. Firstly, the winter diet contains a great deal of indigestible material (shown by metabolizable energy trials), requiring the handling of a greater volume than in summer to obtain a similar amount of nutrients. Secondly, an increase in metabolism in winter through acclimitization (Delane, 1968) would produce an increase in energy, and therefore, food required.

Some of the organs may have additional unique reasons for changing in size. In winter, feeding is over a shorter period than in summer because of the decrease in day length. The crop may increase in capacity to provide a reservoir of food during the night. The ventriculus may not only have more food to grind in winter but winter food is tougher and probably more difficult to macerate than summer food. It is difficult to see why the small intestine did not hypertrophy to the same extent as the other digestive organs. It is possible that the villi length may have increased in winter, as shown by Lewin (1963) in quail, so that the absorptive area may have increased.

8. Growth

Comparison of Figures 2 and 16 shows that the total weight of juveniles in October and November was near that of adults. Since the total body weight and the digestive organs' weights were not significantly different between the two age classes, from December through February, data

of adults and juveniles were combined from this time on. Pheasants, which were nearly full-grown, were found to have larger digestive organs than adults (Kirkpatrick, 1944). This situation does not appear to be true for spruce grouse as the only measurement that was significantly greater in juveniles than adults (December through February) was small intestine length. As some other digestive organs were larger in adults at this time, for example, empty ventriculus, the discrepancies are probably a result of recording individual variations because of small samples. Both captive and wild juveniles (Figures 16 and 18) reached their maximum weight in December indicating that termination of growth of the wild birds at this time was not imposed by the diet. When captive birds were autopsied, excess fat was observed which may account for their weight being greater than that of wild birds.

The weights of liver, empty ventriculus, empty large intestine with cloaca, full small intestine and caecum as well as lengths of caeca, small intestine and large intestine with cloaca reached that of adults by September (Figures 4, 13, 15, 10, 11, 6, 7 and 9 compared to Figure 17). At this time weight of the digestive system was proportionately, though not absolutely, larger in juveniles than in adults. In contrast heart weight, like total weight, was highly significantly less in October and November. From November through February, however, differences between juvenile and adult heart weights were not significant.

Figure 16. Mean weights of spruce grouse under 8 months of age collected from the Swan Hills, Alberta.

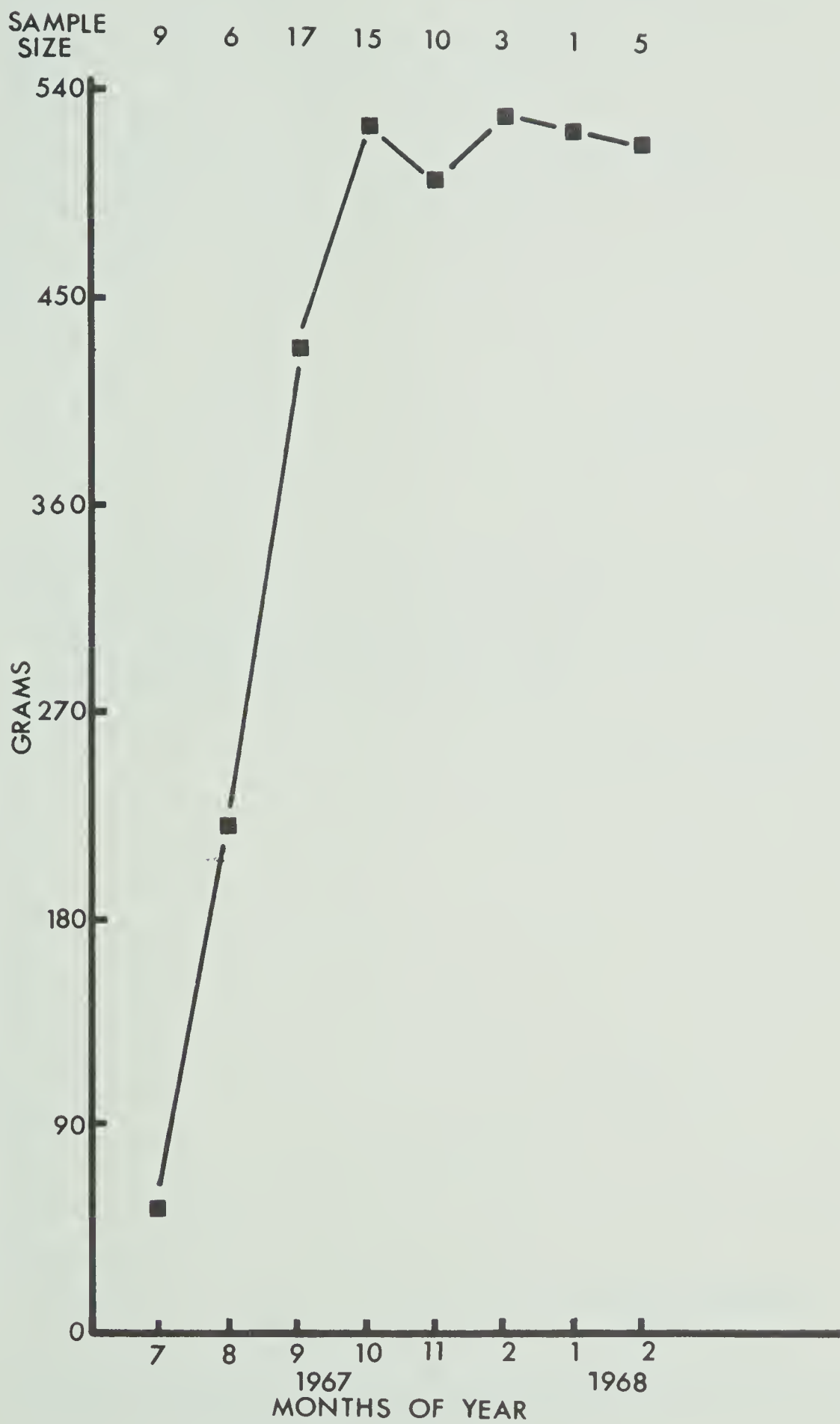


Figure 17. Mean measurements of internal organs of spruce grouse under 8 months of age collected from the Swan Hills, Alberta.

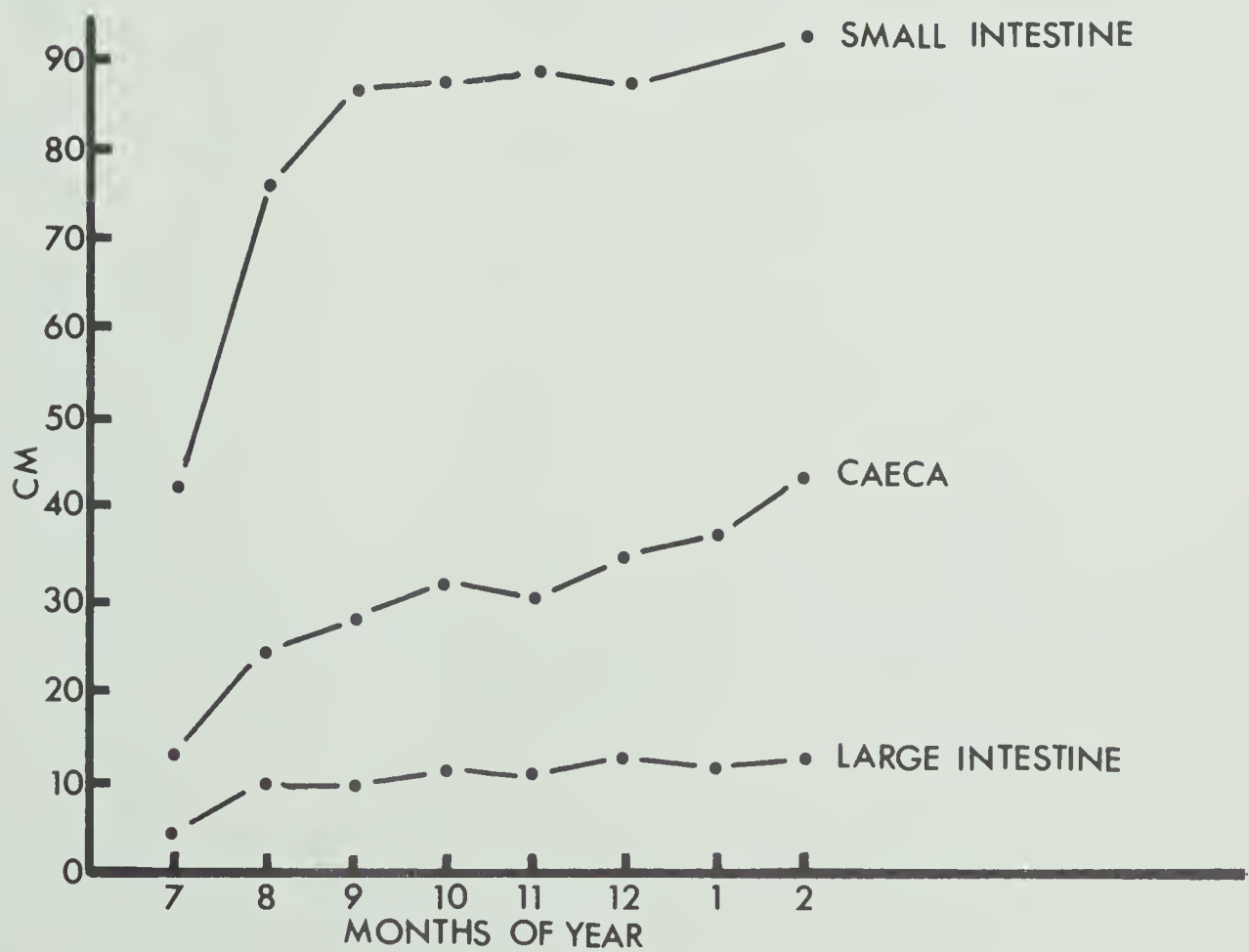
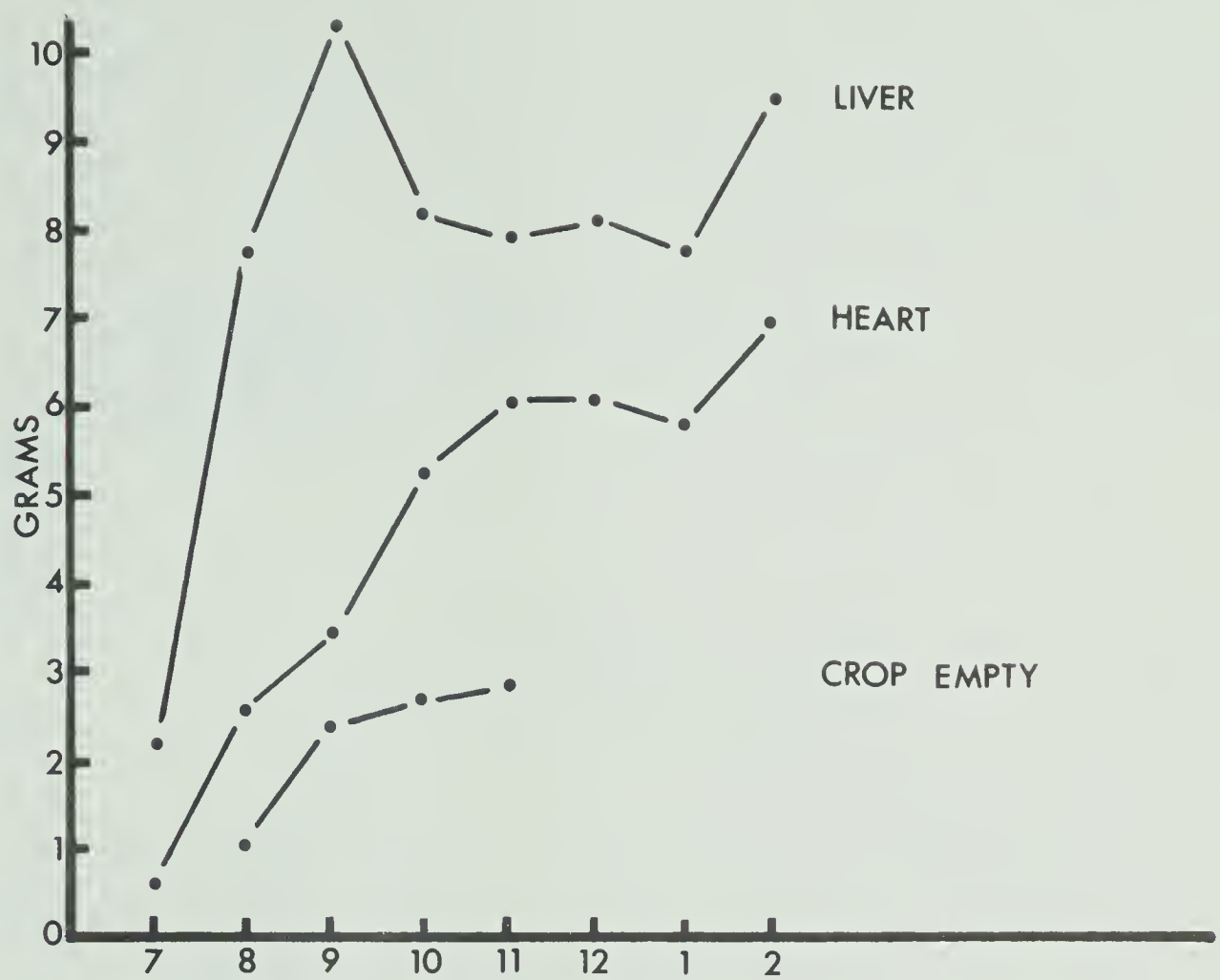
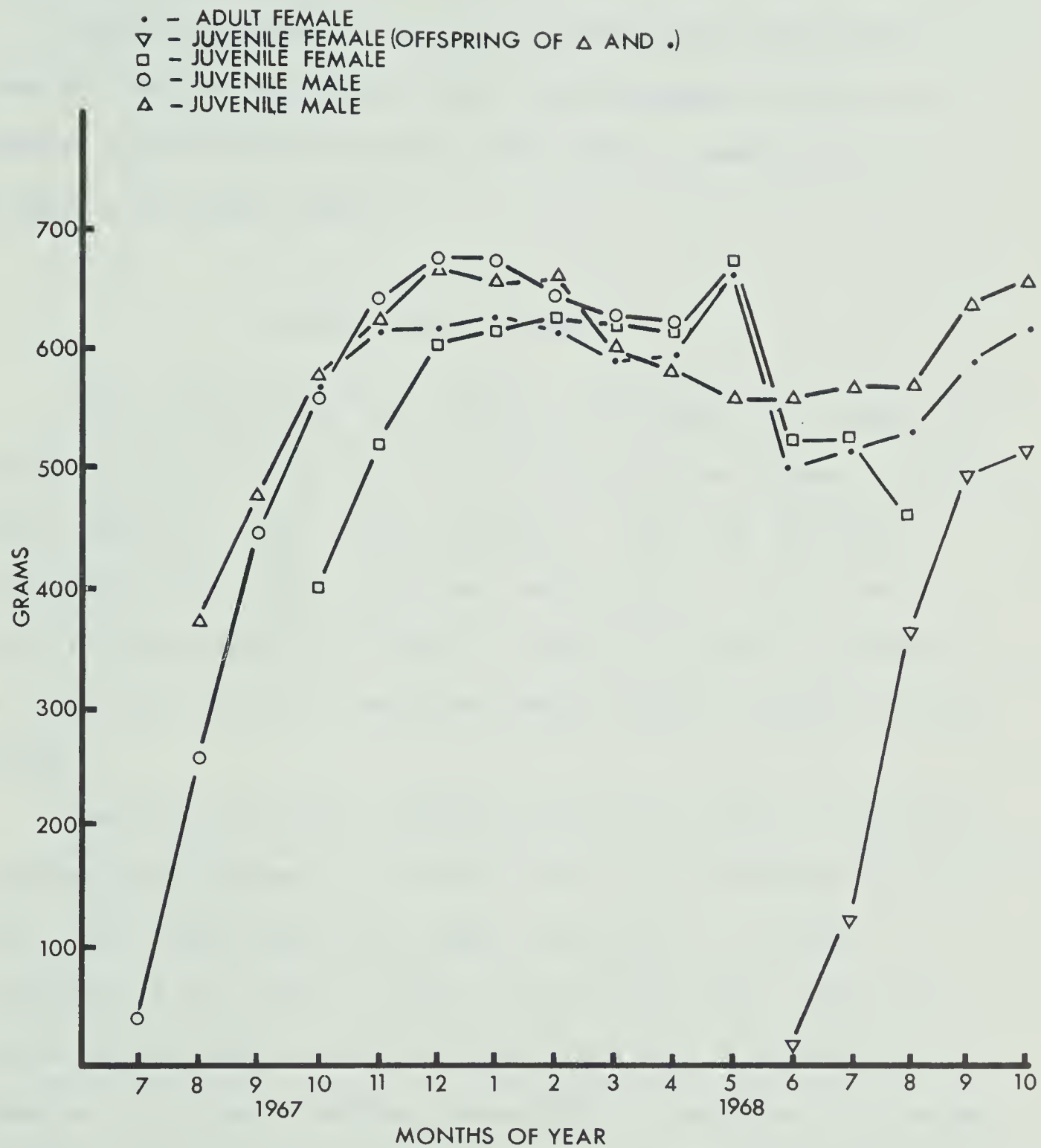


Figure 18. Mean weights of spruce grouse kept in captivity for 9 months or more between July 1967 and October 1968.



Similar differences in rates of growth have been demonstrated in pheasants (Kirkpatrick, 1944) and domestic geese (Roberson and Francis, 1965).

The differences in the measurements of adult and juvenile birds were so slight from December on that it seemed justifiable to group all birds as adults to increase the sample size.

CONCLUDING DISCUSSION

This study taken as a whole, indicated that food was not the controlling factor of spruce grouse numbers during the time and in the place studied. Food was abundant throughout the year and grouse were able to exercise a choice among foods available. The more complex question of food quality, on the other hand, should receive further study.

The spruce grouse studied lived on a diet of conifer needles from November through June, but supplemented this diet with bog cranberries when available in spring. Lodgepole pine needles were the favored winter food in the area studied, but in spring there was a switch by females to spruce needles, possibly in response to changes in calcium and protein requirements. Levels of sodium, phosphorus and calcium were low in most foods consumed by spruce grouse but may have been supplemented by minerals from grit and soil which were found to be consumed in large quantities. The calorie-protein ratio compared to the

requirements of chickens is adequate for maintenance and laying. When the constituent amino acids of the protein were considered the level of methionine was found to be near the marginal level for maintenance and below the requirement for reproduction. However, the methionine level was variable in the eight samples of pine needles analysed for amino acids indicating that for this amino acid the technique of analysis may have been unreliable. Furthermore, other foods (spruce needles and over-wintered bog cranberries) are consumed during reproduction and without amino acid analysis of these foods the significance of the possible low methionine of pine is unknown. Juveniles also utilized over-wintered berries to a large degree in their first month of life, again raising a question of the importance of these berries, but the limited analyses of bog cranberries gave no indication that they are more valuable nutritionally than any other food. Pullianinen *et al.* (1968) nevertheless found them to be highly digestible in willow grouse indicating that they are a good energy source.

If over-wintered berries are necessary for reproduction, periodic fluctuations in their quantity could be important to chick survival, either directly, since they are a food of chicks, or indirectly through an effect on the quality of eggs that produced the chicks. Opposing this suggestion, King (1968) did not find a correlation between spring foods and chick survival in blue grouse.

Crude fiber digestion occurs at a higher rate in the caeca than in the intestines. However, the quantity of crude fiber entering the caeca is so slight, that its digestion there is of no relevance to the total nutritional picture of the grouse. I hypothesize that the main function of these large organs is for the microbiological synthesis of substances such as vitamins, rather than the breakdown of significant quantities of crude fiber. Measurements of vitamins in the contents of the caeca in comparison with the food might give valuable insights into this question.

The problems caused by the high crude fiber content of the food is met by an increase in capacity of the digestive system in winter and by a separation in the ventriculus of the fibrous material from the more easily digested constituents of food, presumably allowing a more efficient digestion. For grouse to be successfully kept in captivity on their natural winter diet, they would have to be conditioned to the diet or captured while on it. This need to adjust to the diet may partly explain the difficulty experienced by Stirling (1965) and Hill *et al.* (1968) in keeping blue grouse and ruffed grouse in captivity on natural winter food. The increase in heart size in winter may facilitate a greater need for circulation to supply the enlarged gut tract. Further investigation might show that acclimatization in the winter may also produce a need for a greater circulation.

No evidence was found of increased mortality of spruce

grouse in winter. It is unlikely that all sick and dying birds would have been missed in sampling, if a die off had occurred. If food is involved in population regulation at all, it appears more likely that this regulation occurs in the reproductive phase of the life cycle rather than the winter phase.

LITERATURE CITED

- Allan, J. A. 1919. Geology of the Swan Hills in Lesser Slave Lake District, Alberta, Canada. Dept. of Mines Geol. Survey Summary Report, 1918, Part C:7-13.
- Baldini, J. T., R. E. Roberts and C. M. Kirkpatrick. 1950. A study of the protein requirements of bobwhite quail reared in confinement in Baller brooders to eight weeks of age. Poul. Sci., 29:291-293.
- Beaton, J., A. Moss, I. MacRae, J. W. Konkin, W. P. McGhee and N. Kosick. 1965. Observations on foliage nutrient content of several coniferous tree species in British Columbia. For. Chron., 41:222-235.
- Boag, D. A. 1963. Significance of location, year, sex, and age to the autumn diet of blue grouse. J. Wildl. Mgmt., 27:555-562.
- _____ 1964. A population study of the blue grouse in southwestern Alberta. Unpub. Ph.D. thesis, Washington State University, Seattle.
- _____ and J. W. Kiceniuk. 1968. Protein and caloric content of lodgepole pine needles. For. Chron., 44:1-3.
- Brody, S. 1964. Bioenergetics and growth. Hafner Publishing Co., Inc. New York.
- Bump, G. R., R. W. Darrow, F. C. Edminster, W. F. Crissey. 1947. The ruffed grouse, life history, propagation management. The Holling Press Inc., Buffalo, New York.

- Crichton, V. 1963. Autumn and winter foods of the spruce grouse in central Ontario. J. Wildl. Mgmt., 27:597.
- Crossley, D. T. 1955. Fruiting habits in lodgepole pine. Canada Dept. No. Aff. and Natl. Resources, Forest Res. Div. Tech. Note 25.
- Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science, 33:43-64.
- Delane, T. M. 1968. Cold temperature adaptations in the ring-necked pheasant, *Phasianus colchicus* and the gray partridge, *Perdix perdix*. Unpub. M.Sc. thesis, University of Alberta, Edmonton.
- Ellison, L. N. 1966. Seasonal foods and chemical analysis of winter diet of Alaskan spruce grouse. J. Wildl. Mgmt., 30:729-735.
- Ewing, R. W. 1947. Poultry nutrition. J. J. Little and Ives Company, New York.
- Forbes, R. M. and W. P. Garrigus. 1948. Application of a lignin ratio technique to the determination of the nutrient intake of grazing animals. J. Anim. Sci., 7:373-382.
- Funk, E. M. 1932. Can the chick balance its ration? Poult. Sci., 11:94-97.
- Godfrey, W. E. 1966. The birds of Canada. Queens Printer, Ottawa.
- Gullion, G. W. 1966. A viewpoint concerning the significance of studies of game bird food habits. Condor, 68:372-476.

- Hill, F. W. and L. M. Dansky. 1954. Studies of the energy requirements of chickens. *Poult. Sci.*, 33:112-119.
- Hill, D. C., E. V. Edwin, H. G. Lumsden. 1968. Metabolizable energy of aspen flower buds for captive ruffed grouse. *J. Wildl. Mgmt.*, 32:854-858.
- Hoffmann, R. S. 1961. The quality of the winter food of blue grouse. *J. Wildl. Mgmt.*, 25:209-210.
- Holmes, J. C. and D. A. Boag. 1965. Parasites of the mountain grouse of Alberta, Canada. *Wjadososci Paraxylotogiczne*, T. SI NR:1-2.
- Irving, I., G. C. West and L. J. Peyton. 1967. Winter feeding program of Alaska willow ptarmigan shown by crop contents. *Condor*, 69:69-77.
- Imondi, D. R. and F. H. Bird. 1965. The sites of nitrogen absorption from the alimentary tract of the chicken. *Poult. Sci.*, 44:916-920.
- Jenkins, D. 1963. Population control in red grouse *Lagopus lagopus scoticus*, 13th Int. Ornith. Cong., 11:690-700.
- King, R. D. 1968. Food habits in relation to the ecology and population dynamics of blue grouse. Unpub. M.Sc. thesis, University of British Columbia, Vancouver.
- Kirkpatrick, C. M. 1944. Body weight and organ measurements in relation to age and season in ring-necked pheasants. *Anat. Rec.*, 89:175-194.
- Klebenow, D. A. and G. M. Gray. 1968. Food habits of juvenile sage grouse. *J. Range Mgmt.*, 21:80-83.

- Korschgen, L. J. 1966. Foods and nutrition of ruffed grouse in Missouri. *J. Wildl. Mgmt.*, 30:86-100.
- Koskimies, J. 1955. Ultimate causes of cyclic fluctuations in numbers in animal populations. *Papers on Game Res.*, 15. Finn. Game Found., Helsinki.
- Lauckhart, J. B. 1957. Animal cycles and food. *J. Wildl. Mgmt.*, 21:230-234.
- Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.
- Lewin, V. 1963. Reproduction and development of young in a population of California quail. *Condor*, 65: 249-278.
- Leopold, A. S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Mgmt.*, 17:197-203.
- Martin, A. C., R. H. Gonsch, and C. P. Brown. 1946. Alternative methods in upland gamebird food analysis. *J. Wildl. Mgmt.*, 10:8-12.
- Maynard, A. B. and J. K. Loosli. 1962. Animal nutrition. McGraw-Hill Book Co. Inc.
- McBee, R. H. and G. C. West. 1969. Caecal fermentation in the willow ptarmigan. *Condor*, 71:54-58.
- McDonald, P., R. A. Edwards, J. E. D. Greenhalgh. 1966. Animal nutrition. Oliver and Boyd, Edinburgh and London.
- Moore, S. and W. H. Stein. 1963. Chromatographic determination of amino acids by the use of automatic recording equipment. *Methods in Enzymology*, 6:819-851.

- Morgan, J. T. and D. Lewis. 1962. Nutrition of pigs and poultry. Butterworths, London.
- Moss, E. H. 1967. Flora of Alberta. University of Toronto Press, Ontario.
- Mueller, W. J. 1956. Feasibility of the chronic oxide and the lignin indicator method for metabolism experiments with chickens. J. Nutrition, 58:29-36.
- National Research Council. 1966. Nutrient Requirements for Domestic Animals. No. 1 Nutrient requirements for Poultry.
- Pullianinen, E., L. Paloheimo and L. Syrjala. 1968. Digestibility of blueberry stems (*Vaccinium myrtillus*) and cowberries (*Vaccinium vitis-idaea*) in the willow grouse (*Lagopus lagopus*). Annales Academiae Scientiarum Fennicae Series A IV Biologica 126 Helsinki, P. 1-15.
- Roberson, D. H. and D. W. Francis. 1965. Anatomical development of white Chinese geese. Poult. Sci., 44:835-839.
- Robel, R. J. and S. A. Linderman. 1966. Weight dynamics of unconfined bobwhite quail in Kansas. Trans. Kansas Acad. Sci., 69:132-138.
- Sadler, K. C. 1961. Grit selectivity by the female pheasant during egg production. J. Wildl. Mgmt., 25:339-341.

- Seiskari, P. 1962. On the winter ecology of the capercaillie, *Tetrao urogallus* and the black grouse, *Lyrurus tetrix* in Finland. Finn. Game Found., Helsinki Unionink 22.
- Siivonen, L. 1957. The problem of the short-term fluctuations in numbers of tetraonids in Europe. Finn. Game Found. Paper on Game Res., 19:1-44.
- Steel, R. G. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co. Inc., New York.
- Stenlund, M. H. and L. T. Magnus. 1951. The spruce hen comes back. The Conserv. Volunteer, 14:20-24.
- Stirling, I. G. 1965. Studies of the holding behaviour and nutrition of captive blue grouse. Unpub. M.Sc. thesis, University of British Columbia, Vancouver.
- Stoneberg, R. P. 1967. A preliminary study of the breeding biology of the spruce grouse in northwestern Montana. Unpub. M.Sc. thesis, University of Montana, Missoula.
- Suomalainen, H. and E. Arhimo. 1945. On the microbial decomposition of cellulose by wild gallinaceous birds (family Tetraonidae). Ornis Fennica, 22:21-23.
- Treichler, R. 1946. Nutrient content of some winter foods of ruffed grouse. J. Wildl. Mgmt., 10:12-17.
- Weber, C. W. and B. L. Reid. 1967. Protein requirements of Coturnix quail to five weeks of age. Poult. Sci., 46:1190-1194.

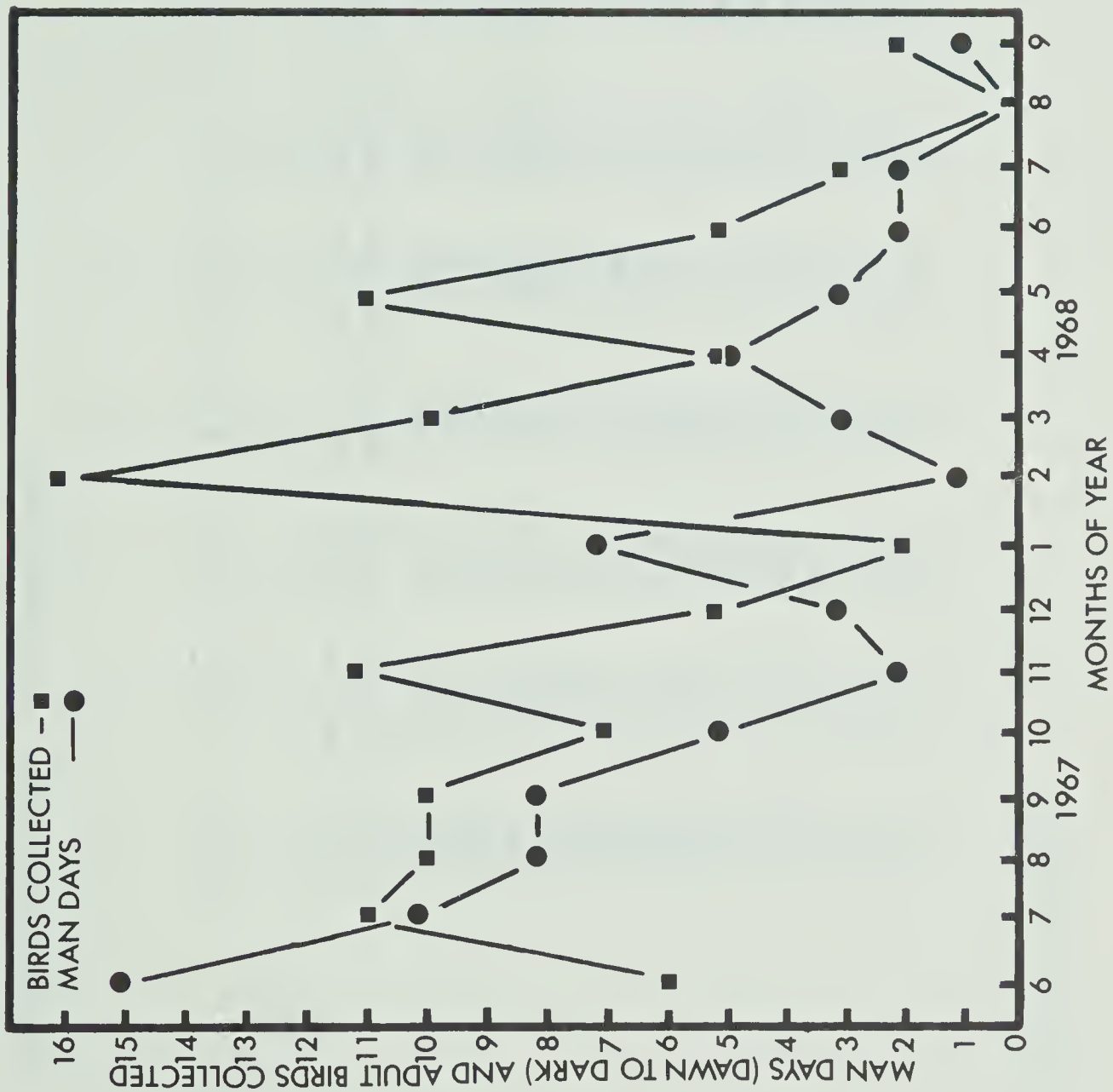
Zwicker, F. C. and J. F. Bendell. 1967. A snare for capturing blue grouse. J. Wildl. Mgmt., 31:202-204.

Zwicker, F. C. 1965. Early mortality and the numbers of blue grouse. Unpub. Ph.D. thesis, the University of British Columbia, Vancouver.

_____ 1966. Winter food habits of capercaillie in northwest Scotland. British Birds, 59:325-336.

APPENDIX I

Time spent each month collecting spruce grouse
and number of grouse collected.



APPENDIX 2. Data from Beckman amino acid analyser.

Sample	1	2	3	4	5	6	7	8
Air dry wt. of pine needle sample (mg)	101.2	97.0	95.6	93.0	102.8	101.5	101.0	102.4
Length of hydrolysis (hr)	12	12	24	24	48	48	72	72
Amino acid	Micro moles	Micro moles	Micro moles	Micro moles	Micro moles	Micro moles	Micro moles	Micro moles
Lysine	.056	.053	.056	.046	.058	.055	.053	.054
Histidine	.016	.017	.016	.013	.018	.017	.018	.016
Arginine	.037	.039	.039	.030	.039	.039	.039	.035
Aspartic acid	.084	.080	.080	.067	.068	.083	.085	.081
Threonine	.044	.043	.028	.025	.042	.039	.035	.039
Serine	.047	.046	.016	.016	.036	.034	.027	.027
Glutamic acid	.087	.089	.090	.072	.094	.093	.071	.094
Proline	.056	.053	.050	.040	.059	.047	.054	.036
Glycine	.094	.088	.094	.080	.101	.096	.102	.092
Alanine	.085	.081	.080	.070	.090	.063	.086	.082
Valine	.064	.061	.064	.057	.072	.069	.068	.067
Methionine	trace	.005	.006	trace	trace	trace	trace	trace
Isoleucine	.047	.046	.049	.039	.052	.048	.050	.046
Leucine	.070	.077	.077	.064	.085	.077	.085	.077
Tyrosine	.013	.016	.019	.014	.011	.016	.017	.014
Phenylalanine	.038	.036	.039	.028	.029	.037	.022	.030

Aliquots analysed are 1/50 of sample hydrolysed
trace = less than .005 micromoles

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